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The evolution of a kleptoparasitic system under adaptive dynamics

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Abstract. Kleptoparasitism, the stealing of food items, is a common biological phenomenon which has been modelled mathematically in a series of recent papers. A common assumption, following early work, was that mixed strategy solutions were not possible. In this paper we consider the evolution of mixed strategies under adaptive dynamics and show that such mixed strategies can be stable solutions under certain assumptions. In particular we revisit the recent paper of Broom et al. (Bull math Biol **66**, 1645–1658, 2004) which assumed pure solutions only, and reanalyze the model under this new formulation.

1. Introduction

When searching for items of food, foragers can find themselves in contact with a conspecific who has discovered such an item. If this item cannot be immediately consumed, then the individual may have the opportunity to steal it. It may or may not be advantageous to make such a stealing attempt, depending on a variety of factors such as the value of the food item, the chance of success and possible costs in entering a contest (e.g. possibility of injury, time or energy used). Hence, food-stealing (kleptoparasitism) falls within the cost-benefit economic framework central to much of behavioural ecology (e.g. [11]). Kleptoparasitism has been observed in many contexts, but is especially common amongst seabirds (e.g. [2,7,22]).

The value of different choices in a kleptoparasitic encounter depend in turn on the choices of others. This obviously occurs in the direct interaction with another individual in any attempted theft, where optimal play can depend upon that of the opponent. However, this is also influenced by the strategies of others not directly involved in the encounter. The relative values of not fighting (either by not challenging or not resisting) and the rewards for success or failure within the contest depend upon the overall food consumption rate of the population, which is heavily dependent upon the strategic choices of individuals. Similarly others may attempt

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to steal the food item from our focal individual, should it successfully take ownership. Thus, the optimal strategy for one individual depends on the optimal strategy for others which provides an ideal situation for game theoretic modelling ([15,14]).

There have been various models of kleptoparasitic behaviour using game theory, examples of which include [1,3,4,21,23]. The most recent game theoretic model of such kleptoparasitic behaviour is [5], which developed the original model of Broom and Ruxton [3] in two ways. Firstly, the probability of success of the challenger was allowed to vary from the original chosen value of one half. Secondly they allowed individuals being challenged to decide not to resist the challenges of others and so forgo a potentially lengthy contest (an important option if the challenger has a high probability of success). This situation allowed different strategic choices and gave rise to three different possible evolutionarily stable strategies (ESSs). These were one where individuals both challenged for food items and resisted challenges from others (Hawk), one where individuals challenged but did not resist (Marauder), and one where individuals did not challenge, but would resist if themselves challenged (Retaliator). It was also possible for two of these to be ESSs under the same ecological conditions. The Marauder ESS is of particular ecological interest, since it involved individuals surrendering valuable items of food in complete absence of dominance hierarchies or intrinsic asymmetries in competitive abilities between individuals. In the following section, we introduce a model which follows on from that of Broom et al. [5], using the same parameters where possible, but where individuals play mixed rather than pure strategies. This model is then analyzed in subsequent sections.

2. The Model

2.1. The model of Broom et al. (2004)

Broom et al. [5] considered a homogeneous population of animals, in which each animal had the option of attempting to steal food from others. Additionally, when attacked whilst handling food, each individual had the option of resisting such an attempted theft. Each individual had to choose a pure option for each of the attacking and defending situations, yielding four types of individual in all.

Hawk – challenge and resist the challenges of others;
Marauder – challenge but do not resist the challenges of others;
Retaliator – do not challenge but resist the challenges of others;
Dove – neither challenge nor resist the challenges of others.

They considered a population where the density of individuals is P. This population is divided into three different activities, the symbols for which will be used to represent both the activity and the density of individuals involved in that particular activity. The density of individuals handling a food item is labelled H, the density of individuals searching for food items and handlers is S and the density involved in an aggressive contest is A. Each of these quantities are determined by the other parameters.

The number of available food items per unit area is given by f. It was assumed that food items take a time to handle drawn from an exponential distribution with mean t_h (i.e. t_h is the expected time for each item of food to be consumed). At the end of handling, the handler resumed searching. When a searcher encountered a handler, it could choose to challenge for the food item, or not. If it did challenge, then the handler could choose to resist, or not. If it did resist, then a fight ensued (with times drawn from an exponential distribution with mean time $t_a/2$). At the end of a contest, the winner started handling the food, and the loser resumed searching. The probability of the challenger winning the contest was given by α.

Individuals were able to search an area ν_f for food in unit time, so that the rate at which individual searchers found food was $\nu_\mathrm{f} f$. Individuals also searched for handlers, being able to search an area of size ν_h per unit time. The rate at which a searcher found handlers was thus $\nu_\mathrm{h} H$.

2.2. *Strategies and evolution*

We develop the model of Broom et al. [5] by allowing the possibility of mixed strategies. We consider a monomorphic population of individuals, each one adopting a strategy $\Sigma = (p, r)$, where p is the probability to attack a handler and r is the probability to retaliate when attacked by a searcher. The parameters that we use in this paper are the same as in [5] where possible. The goal is to find the general conditions for stable strategies, and to identify specific stable strategies in particular situations.

We shall investigate these mixed strategies using adaptive dynamics, first developed by Metz and co-workers (e.g. [16,17]). The rationale of adaptive dynamics in our scenario is as follows. All individuals in the population play the same strategy $\Sigma = \Sigma_\mathrm{p}$. Strategies may change when a mutation occurs in the population and a small fraction of the population changes its strategy to one close to the existing strategy. We shall consider the neighbouring mutant strategy Σ, which is in the direction of maximising the feeding rate of the mutant, equivalent to minimizing $T(\Sigma, \Sigma_\mathrm{p})$ – the time needed from the beginning of searching to the end of handling for the individual adopting the strategy Σ in the population where everybody else adopts the strategy Σ_p (hence the derivative by the first coordinate only and the negative sign in the following equations). Such a mutant has an advantage over the original strategy, and so eventually the mutant replaces the original strategy as the population strategy, i.e. the overall strategy of the population changes in the above manner. For more on adaptive dynamics see [8,18–20]. There are thus three different processes involved in this model, each operating on a different time scale. Individuals have a given strategy for attacking and defending against attackers, and move between the various states (e.g. handling). This occurs on a very short time scale, and we assume that the population reaches a dynamic equilibrium between the states. For a justification of this, see [12]. When a mutation occurs, the population consists of the mutant group, and the (initially much larger) group playing the original strategy. The relative numbers of each type change in successive generations, according to the fitness of each type, until one of the two eliminates the other. This is the intermediate size time scale. New mutations are assumed to occur rarely, on the slowest time scale, so that the result of contests between the previous population strategy and mutant are always resolved before any new mutation.

Table 1. The model parameters and their definitions

Symbol	Meaning
P	Total density of individuals in the population
S	Density of individuals which are searching for food
H	Density of individuals which are handling a food item
A	Density of individuals involved in a contest over food
f	Density of food items per unit area
ν_f	Area that individuals can search for food per unit time
ν_h	Area that individuals can search for handlers per unit time
t_h	Expected handling time (if unchallenged)
$t_a/2$	Expected duration of a contest over food
α	Probability that the challenger wins the contest
T_S	Expected time for a searcher to acquire a food item
T_H	Expected handling time (allowing for challenges)
T	Expected time to acquire and consume a food item
p	Probability that a (specific) searcher will attack a handler
r	Probability that a (specific) handler will resist an attack
Σ	Strategy of a specific individual $\Sigma = (p, r)$
p_p	Probability that an average searcher will attack a handler
r_p	Probability that an average handler will resist an attack
Σ_p	Strategy of an average individual $\Sigma_p = (p_p, r_p)$
H_H	Handler density for all Hawk population, $H_H^2 t_a \nu_h + H_H(1 + \nu_f f t_h) = \nu_f f t_h P$

The adaptive dynamics on the trait Σ_p are given by

$$\frac{d\Sigma_p}{dt} = -\nabla_\Sigma T(\Sigma, \Sigma_p)\,\big|_{\Sigma=\Sigma_p}\,, \tag{1}$$

or in components

$$\frac{dp_p}{dt} = -\frac{\partial}{\partial p} T(p, r, p_p, r_p)\Big|_{p=p_p, r=r_p}, \tag{2}$$

$$\frac{dr_p}{dt} = -\frac{\partial}{\partial r} T(p, r, p_p, r_p)\Big|_{p=p_p, r=r_p}. \tag{3}$$

We will calculate $T(\Sigma, \Sigma_p)$ in two steps. First we will calculate $T_S = T_S(\Sigma, \Sigma_p)$ the time needed to find a food item and begin handling. Second, we will calculate $T_H = T_H(\Sigma, \Sigma_p)$ the time needed to finish handling by eating the food item (when possibly disturbed by other searchers). A summary of the parameters used in our model and their meaning is given in Table 1.

3. General model analysis

3.1. Calculation of T_S

After starting to search, an individual can find food or a handler. We assume that both processes – looking for food and looking for a handler – have exponential distribution with means $(v_\mathrm{f} f)^{-1}$ and $(v_\mathrm{h} H)^{-1}$, respectively. An individual will find something in average time

$$(v_\mathrm{f} f + v_\mathrm{h} H)^{-1}.$$

It will find a handler sooner than food with probability

$$\frac{v_\mathrm{h} H}{v_\mathrm{f} f + v_\mathrm{h} H}.$$

Once a handler is found, the searcher decides whether it will attack or not. If it does not attack, it returns to the searching state (and nothing happens). The probability that a searcher will attack is given by Σ, i.e. p. If the searcher attacks, then the handler has the option whether to resist or not. If the handler does not resist, it gives up food and returns to searching, while the searcher begins to handle. If the handler resists, then there is a fight (that lasts for an average time $t_a/2$) and at the end of the fight, the searcher wins with probability α. The probability that the handler will resist is given by Σ_p, i.e. r_p.

From the above, we have

$$T_S = \frac{1}{v_\mathrm{f} f + v_\mathrm{h} H} + \frac{v_\mathrm{h} H}{v_\mathrm{f} f + v_\mathrm{h} H}\left[(1-p)T_S + pr_\mathrm{p}\frac{t_a}{2} + pr_\mathrm{p}(1-\alpha)T_S\right].$$

It follows that

$$T_S = \frac{1 + v_\mathrm{h} H p r_\mathrm{p}\,(t_a/2)}{v_\mathrm{f} f + v_\mathrm{h} H p(1 - r_\mathrm{p}(1-\alpha))}. \tag{4}$$

From (4) we can calculate the derivatives of T_S by p and r, respectively.

$$\frac{\partial T_S}{\partial p} = \frac{v_\mathrm{h} H\left\{r_\mathrm{p}\left[(t_a/2)\, v_\mathrm{f} f + (1-\alpha)\right] - 1\right\}}{\left(v_\mathrm{f} f + v_\mathrm{h} H p\left(1 - r_\mathrm{p}(1-\alpha)\right)\right)^2}, \tag{5}$$

$$\frac{\partial T_S}{\partial r} = 0. \tag{6}$$

The Eq. (6) is natural since an individual's searching time is unaffected by altering its resistance strategy.

3.2. *Calculation of* T_H

While handling, there are two processes happening, both having the exponential distribution. One is eating (with rate $1/t_\mathrm{h}$), the second one is being looked for by searchers (with finding rate $v_\mathrm{h} S$). Something will happen in (an average time)

$$\frac{1}{\frac{1}{t_\mathrm{h}} + v_\mathrm{h} S} = \frac{t_\mathrm{h}}{1 + t_\mathrm{h} v_\mathrm{h} S}.$$

The handler is found by a searcher before it finishes handling with probability

$$\frac{v_\mathrm{h} S}{(1/t_\mathrm{h}) + v_\mathrm{h} S} = \frac{t_\mathrm{h} v_\mathrm{h} S}{1 + t_\mathrm{h} v_\mathrm{h} S}.$$

When found by a searcher, it may or may not be attacked, an attack happening with probability p_p. If it is not attacked, nothing happens and handling continues. If it is attacked, it can resist or not, resisting with probability r. If it does not resist, the food is lost and it returns to searching (i.e. spends time $T_S + T_\mathrm{H}$ from now to the end of handling). If it resists, there is a fight that takes time $t_a/2$. After that, the handler wins with probability $(1-\alpha)$ and returns to handling (it takes time T_H from now to the end of handling). If it loses (with probability α), it loses the food and returns to searching. From the above, we get

$$T_\mathrm{H} = \frac{t_\mathrm{h}}{1+t_\mathrm{h}v_\mathrm{h}S} + \frac{t_\mathrm{h}v_\mathrm{h}S}{1+t_\mathrm{h}v_\mathrm{h}S}\Bigg[(1-p_\mathrm{p})T_\mathrm{H} + p_\mathrm{p}(1-r)(T_S+T_\mathrm{H}) + p_\mathrm{p}r\left(\frac{t_a}{2} + T_\mathrm{H} + \alpha T_S\right)\Bigg].$$

After simplification we get

$$T_\mathrm{H} = t_\mathrm{h} + t_\mathrm{h}v_\mathrm{h}Sp_\mathrm{p}\Big[T_S(1-r(1-\alpha)) + r\frac{t_a}{2}\Big]. \tag{7}$$

From (7) we can calculate the derivatives.

$$\frac{\partial T_\mathrm{H}}{\partial p} = t_\mathrm{h}v_\mathrm{h}Sp_\mathrm{p}\,(1-r(1-\alpha))\,\frac{\partial T_S}{\partial p}, \tag{8}$$

$$\frac{\partial T_\mathrm{H}}{\partial r} = t_\mathrm{h}v_\mathrm{h}Sp_\mathrm{p}\left[\frac{t_a}{2} - T_S(1-\alpha)\right]. \tag{9}$$

Note that the handling time is affected by the searching strategy since there is the possibility of being challenged and losing and so returning to searching before handling is complete.

3.3. Dependence of S and H on p_p and r_p

In any given time, there is a certain distribution of individuals between states S, H and A. Let us describe how this distribution changes in time. An individual can become a searcher if

(S1) It was a handler and finished eating food (with the rate $1/t_\mathrm{h}$), or
(S2) It was a handler, was found by a searcher, attacked and did not resist (with rate $v_\mathrm{h}Sp_\mathrm{p}(1-r_\mathrm{p})$), or
(S3) It was involved in a fight and lost (with the rate $0.5 \cdot 1/(t_a/2)$, since each individual is equally likely to be challenger or challengee and so will lose half its fights).

An individual can become a handler if

(H1) It was a searcher and found food (with the rate $v_\mathrm{f}f$), or
(H2) It was a searcher and found and attacked a handler that did not resist (with the rate $v_\mathrm{h}Hp_\mathrm{p}(1-r_\mathrm{p})$), or
(H3) It was involved in a fight and won it (with the rate $0.5 \cdot 1/(t_a/2)$, for similar reasoning to (S3)).

An individual can become involved in a fight if

(A1) it was a searcher, found and attacked a handler who did resist (with the rate $v_\mathrm{h} H p_\mathrm{p} r_\mathrm{p}$), or
(A2) it was a handler, was found and attacked by a searcher and did resist (with the rate $v_\mathrm{h} S p_\mathrm{p} r_\mathrm{p}$).

Altogether, S, H and A solve the following differential equations.

$$\begin{aligned}
\frac{\mathrm{d}S}{\mathrm{d}t} &= H \cdot \left(\frac{1}{t_\mathrm{h}} + v_\mathrm{h} S p_\mathrm{p} (1 - r_\mathrm{p}) \right) + \frac{A}{2(t_a/2)} \\
&\quad - S \cdot \left(v_\mathrm{f} f + v_\mathrm{h} H p_\mathrm{p} (1 - r_\mathrm{p}) \right) - S v_\mathrm{h} H p_\mathrm{p} r_\mathrm{p}, \\
\frac{\mathrm{d}H}{\mathrm{d}t} &= -H \cdot \left(\frac{1}{t_\mathrm{h}} + v_\mathrm{h} S p_\mathrm{p} (1 - r_\mathrm{p}) \right) + \frac{A}{2\,(t_a/2)} \\
&\quad + S \cdot \left(v_\mathrm{f} f + v_\mathrm{h} H p_\mathrm{p} (1 - r_\mathrm{p}) \right) - H v_\mathrm{h} S p_\mathrm{p} r_\mathrm{p}, \\
\frac{\mathrm{d}A}{\mathrm{d}t} &= v_\mathrm{h} S H p_\mathrm{p} r_\mathrm{p} + v_\mathrm{h} H S p_\mathrm{p} r_\mathrm{p} - \frac{A}{(t_a/2)}.
\end{aligned}$$

The above equations describe the process on a short timescale (typically a matter of minutes), whereas the equation (1) describes the process on a timescale of many years. Thus when considering (1), we may assume that there is an equilibrium achieved in the above equations (see [12]) i.e.

$$0 = \frac{\mathrm{d}S}{\mathrm{d}t} = \frac{\mathrm{d}H}{\mathrm{d}t} = \frac{\mathrm{d}A}{\mathrm{d}t}.$$

Manipulation of these equations gives

$$H = v_\mathrm{f} f t_\mathrm{h} S, \tag{10}$$

$$A = v_\mathrm{h} H S p_\mathrm{p}\, r_\mathrm{p} t_a = \frac{H^2 t_a v_\mathrm{h} p_\mathrm{p} r_\mathrm{p}}{(v_\mathrm{f} f t_\mathrm{h})}. \tag{11}$$

Since the total density P of individuals in the population remains constant, we get

$$S + H + A = P, \tag{12}$$

and, consequently,

$$H^2 t_a v_\mathrm{h} p_\mathrm{p} r_\mathrm{p} + H(1 + v_\mathrm{f} f t_\mathrm{h}) - v_\mathrm{f} f t_\mathrm{h} P = 0. \tag{13}$$

From (13) we can see that H decreases when $p_\mathrm{p} r_\mathrm{p}$ increases and vice versa. By (10), the same holds for S. By (12), A then increases as $p_\mathrm{p} r_\mathrm{p}$ increases.

3.4. Extreme values of P

We shall briefly look at the two cases P very small, and P very large here, as they are useful for some of the situations that follow. From the Eq. (13) it follows that when P is very low

$$H \approx \frac{v_{\mathrm{f}} f t_{\mathrm{h}} P}{1 + v_{\mathrm{f}} f t_{\mathrm{h}}}.$$

Substituting for H into formula (4), using P is small, we get

$$T_S \approx \frac{1}{v_{\mathrm{f}} f}. \tag{14}$$

Using the above approximation we obtain

$$\frac{\partial T_S}{\partial p} \approx \frac{v_{\mathrm{h}} H \left\{ r_{\mathrm{p}} \left[(t_a/2)\, v_{\mathrm{f}} f + (1-\alpha) \right] - 1 \right\}}{(v_{\mathrm{f}} f)^2} \tag{15}$$

$$= \frac{v_{\mathrm{h}} t_{\mathrm{h}} S}{v_{\mathrm{f}} f} \cdot \left\{ r_{\mathrm{p}} \left[\frac{t_a}{2} v_{\mathrm{f}} f + (1-\alpha) \right] - 1 \right\}. \tag{16}$$

Moreover

$$\frac{\partial T_{\mathrm{H}}}{\partial r} = t_{\mathrm{h}} v_{\mathrm{h}} S p_{\mathrm{p}} \left[\frac{t_a}{2} - T_S (1-\alpha) \right] \tag{17}$$

$$\approx t_{\mathrm{h}} v_{\mathrm{h}} S p_{\mathrm{p}} \left[\frac{t_a}{2} - \frac{1}{v_{\mathrm{f}} f} (1-\alpha) \right], \tag{18}$$

$$\frac{\partial T_{\mathrm{H}}}{\partial p} = t_{\mathrm{h}} v_{\mathrm{h}} S p_{\mathrm{p}} (1 - r(1-\alpha)) \frac{\partial T_S}{\partial p} \approx 0. \tag{19}$$

since this is of order S^2 and thus small compared to $\partial T_S / \partial p$ and $\partial T_{\mathrm{H}} / \partial r$. When the population density P is very high, then Eq. (13) leads to

$$H \approx \sqrt{\frac{P v_{\mathrm{f}} f t_{\mathrm{h}}}{t_a v_{\mathrm{h}} p_{\mathrm{p}} r_{\mathrm{p}}}}.$$

More precisely, for every fixed $\varepsilon > 0$, there is a P_0 such that whenever $P > P_0$, $p_{\mathrm{p}} > \varepsilon$ and $r_{\mathrm{p}} > \varepsilon$, then H is as above. Thus, in our analysis below, we restrict ourself to high density and mixtures where both p_{p} and r_{p} are above (small) ε. (Note that, when P is high, S and H will be large anyway; but if we allow small p_{p} and r_{p}, this complicates our estimate of T_S). For not so small p_{p} and r_{p} we get (using H is large):

$$T_S \approx \frac{r_{\mathrm{p}} (t_a/2)}{1 - r_{\mathrm{p}} (1-\alpha)}. \tag{20}$$

Moreover,

$$\frac{\partial T_S}{\partial p} \approx 0, \tag{21}$$

since it is of order $1/H$. Thus

$$\frac{\partial T_{\mathrm{H}}}{\partial r} = t_{\mathrm{h}} v_{\mathrm{h}} S p_{\mathrm{p}} \left[\left(\frac{t_a}{2} \right) - \frac{r_{\mathrm{p}}(t_a/2)}{1 - r_{\mathrm{p}}(1-\alpha)} (1-\alpha) \right], \tag{22}$$

$$\frac{\partial T_{\mathrm{H}}}{\partial p} = t_{\mathrm{h}} v_{\mathrm{h}} S p_{\mathrm{p}} \left(1 - r(1-\alpha)\right) \frac{\partial T_S}{\partial p} \approx 0. \tag{23}$$

It should also be noted that for very large P the assumptions of our model will break down, especially if there is any challenging for food $p_{\mathrm{p}} > 0$, since the density of individuals is so high that parasitism (with or without fights) will be how most food is acquired and food items will be continually contested before eventually being consumed. Thus the applicability of such results is open to question. On the other hand, it can be seen by comparing the results for large P in the Marauder-Retaliator and Hawk–Dove cases with Figs. 3, 4, 5 and 6 that the solutions that we are able to predict for high densities mathematically, due to simplifications of the equations, actually occur for lower densities as well.

3.5. A relationship between H, T_S and T_{H}

We can establish a direct relationship between the expected total time to find and handle a food item $T_S + T_{\mathrm{H}}$ and the density of handlers H for a population in equilibrium (and in fact this relationship is implicit in several earlier papers including [3] and [5]. The total uptake rate of the population can be expressed in two ways. Firstly each individual spends time $T_S + T_{\mathrm{H}}$ to consume a food item, so the uptake rate is given by $1/(T_S + T_{\mathrm{H}})$. Secondly the proportion of the population in the handling state is H/P and every individual in this state consumes food at rate $1/t_h$ (no others can consume food) so that the mean uptake rate per individual is H/Pt_h. Thus we have

$$\frac{1}{T_S + T_{\mathrm{H}}} = \frac{H}{t_{\mathrm{h}} P}. \tag{24}$$

This relationship follows directly from Eqs. (4), (7), (10) and (13).

4. Mixtures of two pure strategies

4.1. General analysis

In this section we consider the situation where there are some restrictions on the strategies. In particular, we are interested in studying "mixtures of two pure strategies". The strategy state space (described by two variables p and r) will be parameterized by a single variable x. We allow individuals to play a mixture of $\Sigma_1 = (p_1, r_1)$ and $\Sigma_2 = (p_2, r_2)$ with the choice x indicating that an individual plays Σ_1 with probability x, and otherwise plays Σ_2, when either a challenging or defending choice needs to be made. Thus the general set of equations (1) will be simplified to

$$\frac{\mathrm{d}x}{\mathrm{d}t} = -\frac{\partial}{\partial x_1} T(x_1, x) \bigg|_{x_1 = x}. \tag{25}$$

We will be looking for attractors of the above dynamics (25).

In the general framework of adaptive dynamics there can be two types of attracting points – (a) convergent stable strategies (CSSs), see ([6]), and (b) branching points. In both cases, the evolution proceeds in the direction of those points, but they differ by what will happen once the population gets there. The attracting point x_0 is a CSS if it is the best invader of itself (i.e. if the function $T(x, x_0)$ attains its local minimum at x_0). The attracting point x_0 is a branching point, it the population can be invaded by many different mutants. A strategy Σ represented by $0 < x_0 < 1$ will be an attracting point of the dynamics (25), when

1. $\partial/\partial x_1 T(x_1, x_0)|_{x_1=x_0} = 0$,
2. $\partial/\partial x_1 T(x_1, x)|_{x_1=x} > 0$ for x in a right neighborhood of x_0,
3. $\partial/\partial x_1 T(x_1, x)|_{x_1=x} < 0$ for x in a left neighborhood of x_0.

and it will be a CSS if moreover

4. $\partial^2/\partial x_1^2 \, T(x_1, x_0) \,\big|_{x_1=x_0} > 0$.

The strategy $x_0 = 0$ is a CSS if condition (2) is met and the strategy $x_0 = 1$ is a CSS if condition (3) is met.

The analysis of the condition (4) is too complex (see Sect. 4.8), but numerical results suggest that in our case, this condition is satisfied at every attracting point. Thus, every attracting point is automatically a CSS. In particular, we are interested in whether the following statements are true or false

$$A := \frac{\partial}{\partial x_1} T(x_1, 0)\bigg|_{x_1=0} > 0,$$

and

$$B := \frac{\partial}{\partial x_1} T(x_1, 1)\bigg|_{x_1=1} < 0.$$

We indicate by A (B) that statement A (B) is true, and by A^C (B^C) that it is false. If the condition A holds, then the strategy parameterized by $x = 0$ is a CSS – because for x slightly bigger than 0, $\partial/\partial x_1 T(x_1, x)|_{x_1=x} > 0$ and thus there is a pressure to minimize x.

For similar reasons, if B holds, then the strategy parameterized by $x = 1$ is a CSS. If A^C holds, then the population of ($x = 0$)-strategists can be invaded; and for the same reason if B^C holds, then the population of ($x = 1$)-strategists can be invaded.

If both A and B hold, then there are two CSS (parameterized by $x = 0$ and $x = 1$), at least one unstable equilibrium in between and possibly more equilibria. When both A^C and B^C hold, there is at least a mixed CSS in between. This statement is generally true in similar situations, and is only violated when the payoff function is badly behaved in the vicinity of the point where $\partial/\partial x_1 T(x_1, x)|_{x_1=x} = 0$. In fact we can see that there is no such problem here. By (24), the payoff function is given in term of a linear function of H which solves the following quadratic equation.

$$H^2 t_a v_{\mathrm{h}} p(x) r(x) + H(1 + v_{\mathrm{f}} f t_{\mathrm{h}}) - v_{\mathrm{f}} f t_{\mathrm{h}} P = 0, \tag{26}$$

Table 2. A summary of CSS results for all pairwise combinations of the pure strategies Hawk, Retaliator, Marauder and Dove. If a strategy is not mentioned, it is never a CSS for the case in question.

	Hawk and Retaliator
CSS	conditions
Hawk	$\frac{t_a}{2} v_\mathrm{f} f - \alpha < 0$
Retaliator	$\frac{t_a}{2} v_\mathrm{f} f - \alpha > 0$
	Dove and Marauder
Marauder	always
	Dove and Retaliator
No pressure	always
	Hawk and Marauder
Marauder	$\frac{t_a}{2} > \frac{1-\alpha}{v_\mathrm{f} f + v_\mathrm{h} H}$, where $H = \frac{v_\mathrm{f} f t_\mathrm{h} P}{1 + v_\mathrm{f} f t_\mathrm{h}}$;
Hawk	$\frac{t_a}{2} < \frac{(1-\alpha)(1 + v_\mathrm{h} H_H \frac{t_a}{2})}{v_\mathrm{f} f + \alpha v_\mathrm{h} H_H}$;
	Marauder and Retaliator
Marauder	always
Retaliator	$\frac{t_a}{2} v_\mathrm{f} f > \alpha$
Mixed	high P, $\alpha < 1/2$ and $\frac{t_a}{2} v_\mathrm{f} f < \alpha$
	Hawk and Dove
Hawk	$t_a v_\mathrm{f} f - 1 + (2\alpha - 1) \frac{t_a}{2} v_\mathrm{h} H_H < 0$; in particular for $\alpha < 1/2$ and either high P or $t_a v_\mathrm{f} f < 1$
Mixed	$t_a v_\mathrm{f} f - 1 + (2\alpha - 1) \frac{t_a}{2} v_\mathrm{h} H_H > 0$; or for high P

The conditions for the pure solutions are necessary and sufficient. There are only two cases where mixed CSSs can occur, the conditions given in these cases are sufficient but not necessary.

where $p(x) = xp_1 + (1 - x)p_2$ and $r(x) = xr_1 + (1 - x)r_2$. The derivative of H, and thus of the payoff function, is bounded and thus the conditions A^C and B^C ensure a mixed CSS. Theoretically, there may be more than one such mixed CSS.

In the next sections, there is a description of the situation for mixtures of specific pairs of strategy types. We restrict ourselves to combinations of the "corner" strategies which use either $p = 0$ or $p = 1$ and $r = 0$ or $r = 1$. These are the four strategies Hawk, Marauder, Retaliator and Dove from [5]. A summary of the results from these sections is given in Table 2.

4.2. Hawk and Retaliator

Strategies can only be in the form $\Sigma = (x, 1)$, i.e. always resist, attack with probability x. The strategy $(1, 1)$ corresponds to Hawk (the case $x = 1$), the strategy $(0, 1)$ corresponds to Retaliator (the case $x = 0$). By using (5), (8) and by letting $r = r_\mathrm{p} = 1$ we get

$$\begin{aligned}\frac{\partial}{\partial x_1}T(x_1,x)\Big|_{x_1=x} &= \frac{\partial}{\partial x_1}(T_S+T_{\mathrm{H}})(x_1,x)\Big|_{x_1=x}\\ &= \frac{\partial}{\partial x_1}T_S(x_1,x)\Big|_{x_1=x}\cdot(1+t_{\mathrm{h}}v_{\mathrm{h}}Sx\alpha)\\ &= \left[\frac{t_a}{2}v_{\mathrm{f}}f-\alpha\right]\cdot\frac{v_{\mathrm{h}}H\,(1+t_{\mathrm{h}}v_{\mathrm{h}}Sx\alpha)}{(v_{\mathrm{f}}f+v_{\mathrm{h}}Hp\,(1-x(1-\alpha)))^2}.\end{aligned}$$

Therefore the sign of $\partial/\partial x_1 T(x_1,x)|_{x_1=x}$ is given only by the sign of $(t_a/2)\,v_{\mathrm{f}}f-\alpha$. In particular, it does not depend on x itself.

- A is true if and only if $(t_a/2)v_{\mathrm{f}}f-\alpha>0$. In that case Retaliator is the only CSS.
- B is true if and only if $(t_a/2)v_{\mathrm{f}}f-\alpha<0$. In that case, Hawk is the only CSS.
- $A^C\cap B^C$ is true if and only if $(t_a/2)v_{\mathrm{f}}f-\alpha=0$. In this case, there is no selection pressure at all. Note that this is a "degenerate" case, which occurs only with precise coincidence of ecological parameters.

4.3. Dove and Retaliator

The strategy state space is parameterized by $(0,x)$, i.e. individuals never attack, yet they can resist with probability x. We see from Eq. (6) and (9) that

$$\frac{\partial}{\partial x_1}T(x_1,x)\Big|_{x_1=x}=0.$$

There is no selection pressure at all, as no contests occur and individuals simply forage.

4.4. Dove and Marauder

The strategy state space is parameterized by $(x,0)$. It means that individuals do not resist at all. The case $x=0$ corresponds to Dove, case $x=1$ corresponds to Marauder. From (5) and (8) we get

$$\frac{\partial}{\partial x_1}T_S(x_1,x)\Big|_{x_1=x}=-\frac{v_{\mathrm{h}}H}{(v_{\mathrm{f}}f+v_{\mathrm{h}}Hx)^2}<0$$

and

$$\frac{\partial}{\partial x_1}T_{\mathrm{H}}(x_1,x)\Big|_{x_1=x}=\frac{\partial}{\partial x_1}T_S(x_1,x)\Big|_{x_1=x}\cdot t_{\mathrm{h}}v_{\mathrm{h}}Sx<0.$$

Thus

$$\frac{\partial}{\partial x_1}T(x_1,x)\Big|_{x_1=x}<0,$$

for all x. It means that under all circumstances it is better to attack more and more, i.e. Marauder is the only CSS.

4.5. Hawk and Marauder

The strategy space is parameterized by $(1, x)$, i.e. individuals always attack and they resist with probability x. The case $x = 0$ corresponds to Marauder, the case $x = 1$ corresponds to Hawk. By (6) and (9) we get

$$\begin{aligned}\frac{\partial}{\partial x_1} T(x_1, x)\Big|_{x_1=x} &= \frac{\partial}{\partial x_1}(T_\text{S} + T_\text{H})(x_1, x)\Big|_{x_1=x}\\ &= 0 + t_\text{h} v_\text{h} S\left[\left(\frac{t_a}{2}\right) - T_\text{S}(x, x)\cdot(1-\alpha)\right].\end{aligned}$$

The sign of $\partial/\partial x_1 T(x_1, x)|_{x_1=x}$ depends only on the sign of

$$\left(\frac{t_a}{2}\right) - T_\text{S}(x, x)(1-\alpha).$$

It corresponds to comparing $(t_a/2) + \alpha T_S(x, x)$ (the average time to become a handler from the point of attack if it decides to resist) to $T_S(x, x)$ (average time to become a handler from the point of attack if it decides not to resist). Since

$$T_S(x, x) = \frac{1 + v_\text{h} H x\,(t_a/2)}{v_\text{f} f + v_\text{h} H(1 - x(1-\alpha))}, \tag{27}$$

we can conclude that

- A holds if and only if $(t_a/2) - \left(\frac{1}{v_\text{f} f + v_\text{h} H}\right)(1-\alpha) > 0$. In this case, Marauder is a CSS.
- B holds if and only if $(t_a/2) - \frac{1 + v_\text{h} H(t_a/2)}{v_\text{f} f + \alpha v_\text{h} H}(1-\alpha) < 0$. In this case, Hawk is a CSS.

Let us denote H_M and H_H, as the density of handlers in the population of Marauders ($x = 0$), and Hawks ($x = 1$), respectively. The exact values of H_M and H_H can be found from (13), so that we have the exact conditions on Hawk and Marauder respectively to be a CSS. Values of H_M and H_H were developed in [3] and H_M essentially follows as well from [9]. We now show that at least one of A and B has to be true. If both are false, then

$$\left(\frac{t_a}{2}\right) - \frac{1 + v_\text{h} H_H\,(t_a/2)}{v_\text{f} f + \alpha v_\text{h} H_\text{H}}(1-\alpha) \;>\; 0$$

and

$$\left(\frac{t_a}{2}\right) - \frac{1}{v_\text{f} f + v_\text{h} H_M}(1-\alpha) < 0$$

which implies

$$\frac{1}{v_\text{f} f + v_\text{h} H_\text{M}}(1-\alpha) > \frac{1 + v_\text{h} H_\text{H}\,(t_a/2)}{v_\text{f} f + \alpha v_\text{h} H_\text{H}}(1-\alpha).$$

The latter, however, can not be true because, by (13),

$$\frac{\partial H}{\partial x} < 0, \tag{28}$$

and, in particular, $H_{\mathrm{M}} > H_{\mathrm{H}}$. We can conclude always at least one of Hawk or Marauder is a CSS. We show below that it is not possible to have a mixed CSS. If x_0 is such a mixed CSS, then

$$\left(\frac{t_a}{2}\right) - T_S(x_0, x_0)(1-\alpha) = 0,$$

(which can, theoretically, happen) and $(t_a/2) - T_S(x, x)(1-\alpha)$ is an increasing function. The latter, however, can not happen because $T_S(x, x)$ is an increasing function for x in the neighborhood of x_0. This follows from (27), (28) and the fact that Hx is increasing, by (26).

For very low P, using an estimate $T_S \approx 1/v_{\mathrm{f}} f$, we get that

- A holds and Marauder is a CSS if and only if $(t_a/2)v_{\mathrm{f}} f \geq 1-\alpha$,
- B holds and Hawk is a CSS if and only if $(t_a/2)v_{\mathrm{f}} f < 1-\alpha$.

In particular, there is only one CSS.

When the density P is high, we obtain the following:

- A holds always, because H is high and thus $(t_a/2) - (1-\alpha)/(v_{\mathrm{f}} f + v_{\mathrm{h}} H)$ $(t_a/2) > 0$. Hence, Marauder is always a CSS for large P.
- B holds (for high P) if and only if $\alpha < 1/2$. In this case Hawk is a CSS.

From (20), we get (for not so small x)

$$\begin{aligned}\left(\frac{t_a}{2}\right) - T_S(x, x)(1-\alpha) &\approx \left(\frac{t_a}{2}\right) - \frac{x\,(t_a/2)}{1-x(1-\alpha)}(1-\alpha)\\ &= \left(\frac{t_a}{2}\right)\cdot\frac{1-2x(1-\alpha)}{1-x(1-\alpha)}.\end{aligned}$$

Thus, for $\alpha < 1/2$,

$$\left(\frac{t_a}{2}\right) - T_S(1, 1)(1-\alpha) \approx \left(\frac{t_a}{2}\right)\cdot\frac{2\alpha-1}{\alpha} < 0.$$

Let us conclude this section with an interesting result which illustrates one difference between low- and high-density populations. It was shown above that we can have two CSSs (Marauder and Hawk) in large populations when $\alpha < 1/2$, yet only one CSS in small populations. The reason for this is as follows. Marauder always emerges as a CSS in large populations. Indeed, encounters are very common and it is beneficial not to try to defend food items, because it means spending $(t_a/2)$ fighting, while it takes virtually no time to acquire another food item by searching (very likely, an individual will find one of the many handlers, who will give up the food).

Hawk can be a CSS in large populations as well: once everybody in the population resists, it does not make much sense to resist less (in particular when $\alpha < 1/2$, i.e. handlers have good chances to win) because it would mean giving up food that is very difficult to obtain - in a large population it is more likely to find a handler than food, thus a searcher has to attack a lot of handlers and lose significant time by fighting before acquiring the food.

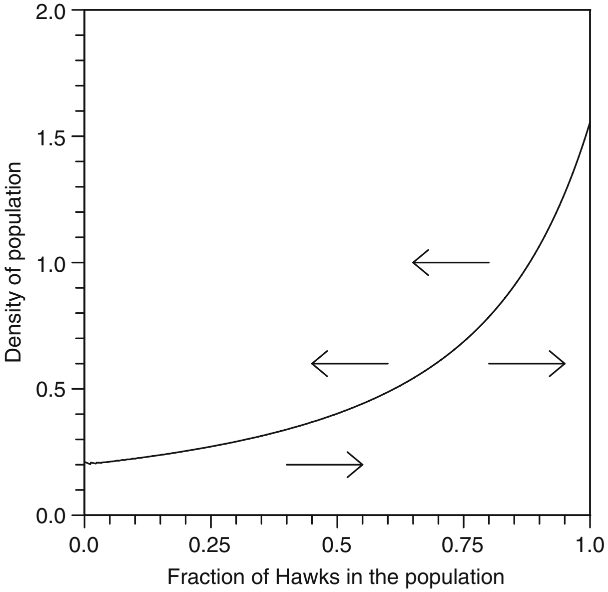

Fig. 1. Dependence of the dynamics on P in Hawk–Marauder population, $t_a = 1$, $v_f f = 0.1$, $t_h = 5$, $v_h = 9$, $\alpha = 0.65$

However, in a small population, encounters between handlers and searchers are very rare (of the order SH i.e. of the order of P^2). Thus the time for acquiring food is (approximately) the same for Hawk and for Marauder and the choice of the strategy depends only on minimizing the handling time. It is very likely that a handler is not found at all or is found at most once during its handling. It may or may not be beneficial to resist this single attempt of a searcher to steal the food. If there is plenty of food (i.e. $1/v_f f$ is small), then it is better for a handler to give up the food and find a new item (Marauder is a CSS). If there is less food, it is more beneficial to resist (Hawk is a CSS).

Notice from Fig.1 that keeping all parameters the same and changing only the density, one gets a change in the dynamics - from low densities and Hawk the only CSS to high densities with Marauder the only CSS, through the transition period where both Hawk and Marauder are CSSs. Figure 2 shows that the coexistence of two CSSs Hawk and Marauder is possible for high densities as well.

4.6. Marauder and Retaliator

The strategy space is parameterized by $(x, 1 - x)$. The case $x = 0$ corresponds to Retaliator, the case $x = 1$ corresponds to Marauder. By (6) and (9) we get

$$\frac{\partial}{\partial x_1} T_S(x_1, x)\bigg|_{x_1 = x} = \frac{\{(1 - x)\,[(t_a/2)v_f f + (1 - \alpha)] - 1\} \cdot v_h H}{(v_f f + v_h H x(1 - (1 - x)(1 - \alpha)))^2}$$

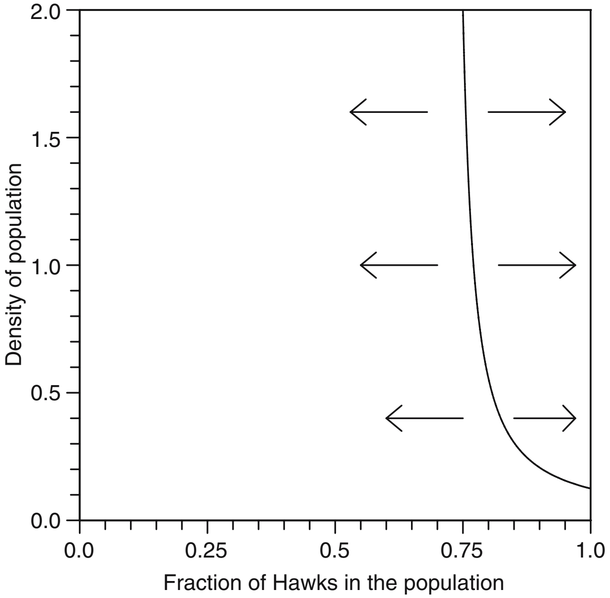

Fig. 2. Dependence of the dynamics on P in Hawk–Marauder population, $t_a = 2$, $v_\mathrm{f} f = 1$, $t_\mathrm{h} = 5$, $v_\mathrm{h} = 9$, $\alpha = 0.3$

$$\begin{aligned}\frac{\partial}{\partial x_1} T_\mathrm{H}(x_1, x)\Big|_{x_1=x} &= \frac{\partial T_\mathrm{H}}{\partial p} - \frac{\partial T_\mathrm{H}}{\partial r}\\ &= t_\mathrm{h} v_\mathrm{h} S x \left[\frac{\partial}{\partial x_1} T_S(x_1, x)\Big|_{x_1=x} \cdot (1-(1-x)(1-\alpha)) \right.\\ &\quad \left. + T_S(x, x)\cdot(1-\alpha) - \frac{t_a}{2}\right]\end{aligned}$$

From the above formulas, the following follows.

- A holds and Retaliator is a CSS if and only if $(t_a/2)v_\mathrm{f} f - \alpha > 0$,
- B holds and Marauder is a CSS always.

Indeed, for $x = 0$, we have $\partial/\partial x_1 T_\mathrm{H}(x_1, 0)|_{x_1=0} = 0$ and thus the sign of $\partial/\partial x_1 T(x_1, 0)|_{x_1=0}$ depends only on the sign of $(t_a/2)v_\mathrm{f} f - \alpha$. For $x = 1$, we get

$$\frac{\partial}{\partial x_1} T_S(x_1, 1)\Big|_{x_1=1} = -\frac{v_\mathrm{h} H}{(v_\mathrm{f} f + v_\mathrm{h} H)^2},$$

and thus

$$\frac{\partial}{\partial x_1} T_\mathrm{H}(x_1, 1)\Big|_{x_1=1} = t_h v_\mathrm{h} S \cdot \left(-\frac{v_\mathrm{h} H}{(v_\mathrm{f} f + v_\mathrm{h} H)^2} + \frac{1}{v_\mathrm{f} f + v_\mathrm{h} H} \cdot (1-\alpha) - \frac{t_a}{2} \right).$$

Thus,

$$\begin{aligned}\frac{\partial}{\partial x_1}T(x_1,1)\Big|_{x_1=1} &= \frac{-v_{\mathrm{h}}H + t_{\mathrm{h}}v_{\mathrm{h}}S\,[-v_{\mathrm{h}}H + (v_{\mathrm{f}}f + v_{\mathrm{h}}H)(1-\alpha)]}{(v_{\mathrm{f}}f + v_{\mathrm{h}}H)^2} \\ &\quad - t_{\mathrm{h}}v_{\mathrm{h}}S\left(\frac{t_a}{2}\right) \\ &< \frac{-v_{\mathrm{h}}H - t_{\mathrm{h}}v_{\mathrm{h}}Sv_{\mathrm{h}}H + (v_{\mathrm{f}}f + v_{\mathrm{h}}H)t_{\mathrm{h}}v_{\mathrm{h}}S}{(v_{\mathrm{f}}f + v_{\mathrm{h}}H)^2} \\ &= \frac{-v_{\mathrm{h}}H + v_{\mathrm{f}}f t_{\mathrm{h}}v_{\mathrm{h}}S}{(v_{\mathrm{f}}f + v_{\mathrm{h}}H)^2} = 0.\end{aligned}$$

The last equality holds by (10).

For small P, using (18) and (10),

$$\begin{aligned}\frac{\partial}{\partial x_1}T(x_1,x)\Big|_{x_1=x} &\approx \frac{t_{\mathrm{h}}v_{\mathrm{h}}S}{v_{\mathrm{f}}f}\cdot\left\{(1-x)\left[\left(\frac{t_a}{2}\right)v_{\mathrm{f}}f + (1-\alpha)\right] - 1\right. \\ &\qquad \left. + x(1-\alpha) - xv_{\mathrm{f}}f\left(\frac{t_a}{2}\right)\right\} \\ &= \frac{t_{\mathrm{h}}v_{\mathrm{h}}S}{v_{\mathrm{f}}f}\cdot\left[\left(\frac{t_a}{2}\right)v_{\mathrm{f}}f(1-2x) - \alpha\right].\end{aligned}$$

Thus, if $(t_a/2)v_{\mathrm{f}}f(1-2x) - \alpha < 0$, increasing x is optimal; if $(t_a/2)v_{\mathrm{f}}f(1-2x) - \alpha > 0$, decreasing x is optimal. This means that the only candidate for a mixed CSS,

$$x_0 = \frac{1}{2}\left(1 - \frac{\alpha}{(t_a/2)\,v_{\mathrm{f}}f}\right)$$

is not stable and thus there is no mixed CSS.

For large P, by (21), (23) and (22), recalling that these results are only valid for $x > \epsilon$, we get

$$\begin{aligned}\frac{\partial}{\partial x_1}T(x_1,x)\Big|_{x_1=x} &\approx t_{\mathrm{h}}v_{\mathrm{h}}Sx\left(T_S(x,x)(1-\alpha) - \frac{t_a}{2}\right) \\ &\approx t_{\mathrm{h}}v_{\mathrm{h}}Sx\left(\frac{(1-x)\,(t_a/2)}{1-(1-x)(1-\alpha)}(1-\alpha) - \frac{t_a}{2}\right) \\ &= \frac{t_{\mathrm{h}}v_{\mathrm{h}}Sx}{1-(1-x)(1-\alpha)}\cdot\left(\frac{t_a}{2}\right)\cdot\left(2(1-x)(1-\alpha) - 1\right).\end{aligned}$$

Recall that due to our estimate (20) of T_S, this approximation does not work too close to Marauder (r_{p} would be too small) nor Retaliator (p_{p} would be too small).

Since $\partial/\partial x_1 T(x_1,x)|_{x_1=x} < 0$, for $\alpha \geq 1/2$, there are no mixed CSS in the region $(\varepsilon, 1-\varepsilon)$. In fact, the population tends to Marauder (although we have not proved that it will reach it).

If $\alpha < 1/2$, then $\partial/\partial x_1 T(x_1,x)|_{x_1=x} > 0$ for x relatively small (yet greater than ε.) This means, that if $\partial/\partial x_1 T(x_1,0)|_{x_1=0} < 0$, there is a mixed CSS somewhere close to Retaliator (x has to be smaller than ε). This occurs when $(t_a/2)v_{\mathrm{f}}f - \alpha < 0$,

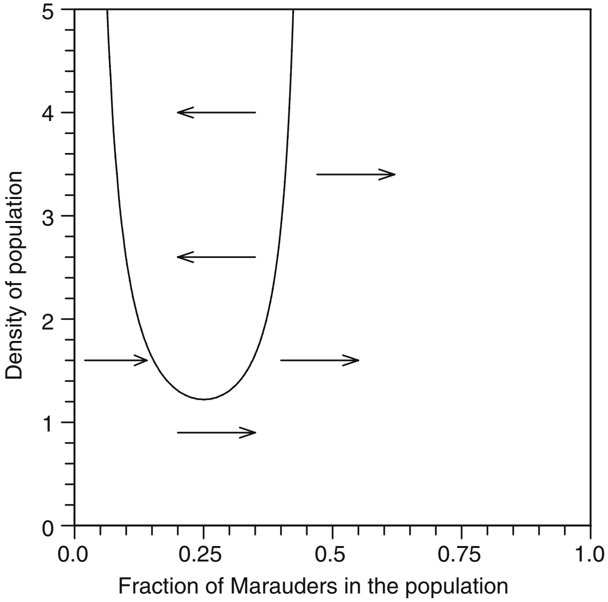

Fig. 3. Dependence of the dynamics on P in Marauder–Retaliator population, $t_a = 1$, $v_\mathrm{f} f = 0.1$, $t_\mathrm{h} = 5$, $v_\mathrm{h} = 9$, $\alpha = 0.06$

i.e. precisely when Retaliator is not a CSS. Note that this does not rule out the possibility of multiple mixed CSSs, but it is clear that there is at least one. We can see the effect of changing the density P on the CSS solutions of this case in Fig. 3. Figure 4 illustrates that both Marauder and Retaliator can be CSSs at the same time.

4.7. Hawk–Dove

The strategy state is parameterized by (x, x). The case $x = 0$ corresponds to Dove, the case $x = 1$ corresponds to Hawk. By (6) and (9) we get

$$\begin{aligned}
\frac{\partial}{\partial x_1} T_S(x_1, x)\bigg|_{x_1=x} &= \frac{\{x\,[(t_a/2)\,v_\mathrm{f} f + (1-\alpha)] - 1\} \cdot v_\mathrm{h} H}{(v_\mathrm{f} f + v_\mathrm{h} H x(1 - x(1-\alpha)))^2} \\
\frac{\partial}{\partial x_1} T_\mathrm{H}(x_1, x)\bigg|_{x_1=x} &= \frac{\partial T_\mathrm{H}}{\partial p} + \frac{\partial T_\mathrm{H}}{\partial r} \\
&= t_\mathrm{h} v_\mathrm{h} S x \left[\frac{\partial}{\partial x_1} T_S(x_1, x)\bigg|_{x_1=x} \cdot (1 - x(1-\alpha)) \right. \\
&\qquad \left. - T_S(x, x) \cdot (1-\alpha) + \left(\frac{t_a}{2}\right) \right]
\end{aligned}$$

Hence,

$$\frac{\partial}{\partial x_1} T(x_1, 0)\bigg|_{x_1=0} < 0$$

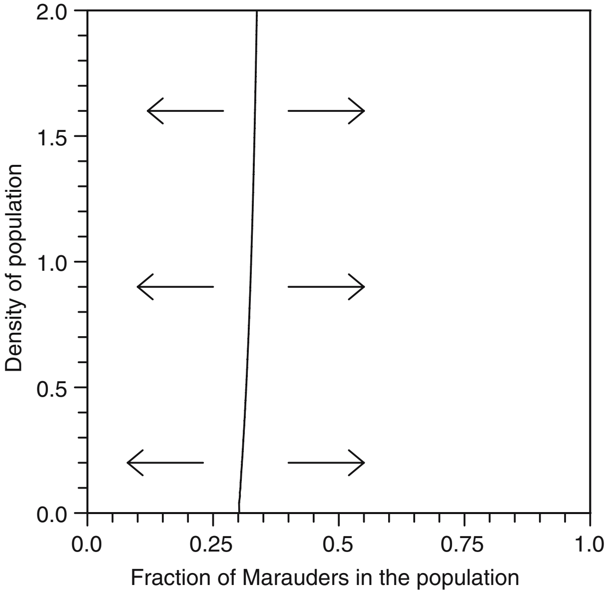

Fig. 4. Dependence of the dynamics on P in Marauder–Retaliator population, $t_a = 1$, $v_{\mathrm{f}} f = 1$, $t_{\mathrm{h}} = 5$, $v_{\mathrm{h}} = 9$, $\alpha = 0.2$

because $\partial/\partial x_1 T_S(x_1, 0)|_{x_1=0} < 0$ and $\partial/\partial x_1 T_{\mathrm{H}}(x_1, 0)|_{x_1=0} = 0$. Hence Dove is never a CSS (it can be invaded by more aggressive individuals, condition A^C). Let us check the sign of $\partial/\partial x_1 T(x_1, 1)|_{x_1=1}$. Substituting $x = 1$ and $S = H/v_{\mathrm{f}} f t_h$ into the above equations we get

$$\begin{aligned}
\frac{\partial}{\partial x_1} T(x_1, 1)\Big|_{x_1=1} &= \frac{\partial}{\partial x_1} T_{\mathrm{S}}(x_1, 1)\Big|_{x_1=1} + \frac{\partial}{\partial x_1} T_H(x_1, 1)\Big|_{x_1=1} \\
&= \left(1 + \frac{\alpha v_{\mathrm{h}} H}{v_{\mathrm{f}} f}\right)\left\{\left(\frac{t_a}{2}\right) v_{\mathrm{f}} f - \alpha\right\} \cdot \frac{v_{\mathrm{h}} H}{(v_{\mathrm{f}} f + v_{\mathrm{h}} H \alpha)^2} + \\
&\quad \left(\frac{t_a}{2}\right) \frac{v_{\mathrm{h}} H}{v_{\mathrm{f}} f} - \frac{(1-\alpha) v_{\mathrm{h}} H}{v_{\mathrm{f}} f} \cdot \frac{1 + v_{\mathrm{h}} H\,(t_a/2)}{v_{\mathrm{f}} f + v_{\mathrm{h}} H \alpha} \\
&= \frac{v_{\mathrm{h}} H}{v_{\mathrm{f}} f (v_{\mathrm{f}} f + \alpha v_{\mathrm{h}} H)} \left(t_a v_{\mathrm{f}} f - 1 + (2\alpha - 1)\left(\frac{t_a}{2}\right) v_{\mathrm{h}} H\right)
\end{aligned}$$

So that B is satisfied and Hawk is a CSS if

$$t_a v_{\mathrm{f}} f - 1 + (2\alpha - 1)\frac{t_a}{2} v_{\mathrm{h}} H_H < 0$$

and conversely (since A^C holds) there is at least one mixed Hawk-Dove CSS if B^C holds.

For small P we get

$$\begin{aligned}\frac{\partial}{\partial x_1}T(x_1,x)\Big|_{x_1=x} &= \frac{v_{\mathrm{h}}t_{\mathrm{h}}S}{v_{\mathrm{f}}f}\cdot\left\{x\left[\left(\frac{t_a}{2}\right)v_{\mathrm{f}}f+(1-\alpha)\right]-1\right.\\ &\qquad\left.+x\left[-(1-\alpha)+\left(\frac{t_a}{2}\right)v_{\mathrm{f}}f\right]\right\}\\ &= \frac{t_{\mathrm{h}}v_{\mathrm{h}}S}{v_{\mathrm{f}}f}\left[2x\left(\frac{t_a}{2}\right)v_{\mathrm{f}}f-1\right].\end{aligned}$$

Thus

- Hawk is the only CSS if $t_a v_{\mathrm{f}} f < 1$,
- There is a mixed CSS if $t_a v_{\mathrm{f}} f > 1$; the mixture is at $x_0 = 1/(t_a v_{\mathrm{f}} f)$,
- There is always only one CSS [since $\partial/\partial x_1 T(x_1,x)|_{x_1=x}$ is increasing in x].

It may seem strange that this does not depend on α. However, individuals must choose either to attack and defend, or to do neither. When population density is low, an individual is unlikely to face any contests, with a small probability of a single contest, equally likely to occur as a defender or attacker (and with essentially 0 chance of being challenged again at the end of the contest). Therefore its probability of emerging a winner of an average contest is 0.5 whatever the value of α.

For large P, similarly to the case Marauder-Retaliator (and again recalling that the results are only valid for $x > \epsilon$), we get

$$\begin{aligned}\frac{\partial}{\partial x_1}T(x_1,x)\Big|_{x_1=x} &\approx t_{\mathrm{h}}v_{\mathrm{h}}Sx\left(\frac{t_a}{2}-T_S(x,x)(1-\alpha)\right)\\ &= \frac{t_{\mathrm{h}}v_{\mathrm{h}}Sx\,(t_a/2)}{1-x(1-\alpha)}\cdot\Big(1-2x(1-\alpha)\Big).\end{aligned}$$

Hence, $\partial/\partial x_1 T(x_1,x)|_{x_1=x} > 0$, for x close to 0. Since $\partial/\partial x_1 T(x_1,0)|_{x_1=0} < 0$ by general calculations, there must be a mixed CSS somewhere close to Dove (independently of any other parameter). Note, again, that we cannot rule out multiple mixed CSSs here.

When $\alpha > 1/2$, then $\partial/\partial x_1 T(x_1,x)|_{x_1=x} > 0$ for all x close to 1, in particular, Hawk is not a CSS. If $\alpha < 1/2$, then $\partial/\partial x_1 T(x_1,x)|_{x_1=x} < 0$ around $x = 1$, thus Hawk is a CSS.

The mixed solution here is what we would expect, analogous to the classical Hawk Dove game ([14,15]). The pure Hawk solution for large populations is initially surprising, however, since there will be many fights and the uptake rate is low. The explanation lies in the fact that when the defender usually wins ($\alpha < 1/2$), it is optimal to defend your food rather than give it up–there are many potential challengers, so an individual will probably face many such contests. However, giving up the food would be worse, because there are a lot of handlers that will defend (relatively successfully, $\alpha < 1/2$) their food and thus it is very time consuming to actually acquire a food item. (This is a similar argument to that for Hawk to be a CSS in the Hawk–Marauder case with large P). This kind of parameter combination is ideal for the strategy Retaliator, which we have disallowed here.

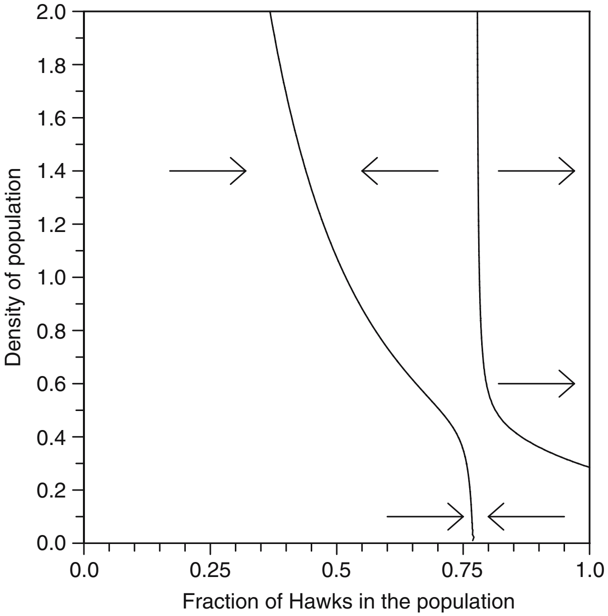

Fig. 5. Dependence of the dynamics on P in Hawk–Dove population, $t_a = 1.3$, $v_\mathrm{f} f = 1$, $t_\mathrm{h} = 5$, $v_\mathrm{h} = 9$, $\alpha = 0.355$

Together:

- There is always a mixed CSS (close to Dove),
- If $\alpha < 1/2$, then Hawk is a CSS.

The effect of varying the density P on the CSSs of the system can be seen in Fig. 5 and Fig. 6. In both figures for low values of P there is just a mixed CSS, and for high values there is a mixed CSS and a pure Hawk CSS, but intermediate behaviour is different. A small change in the parameter α can create a significant change in the dynamics, particularly for low values of P. In fact the condition for Hawk to be a CSS is fairly straightforward, with Hawk being a CSS if and only if P is above a certain value for some parameter combinations, or if and only if P is below a certain value for others. Mixed CSSs always occur for high P, and occur for low P if and only if Hawk is not a CSS, as in Fig. 5 and Fig. 6. However the mixed CSS can disappear for intermediate values, and the interplay between the boundaries for a mixed CSS and for a Hawk varies, giving a variety of possible intermediate behaviours.

Figure 7 shows the situation where Hawk is the CSS for small populations only.

4.8. Second derivatives

This section contains formulas needed for establishing the fact that, in our situation, every inner attracting point is actually a CSS.

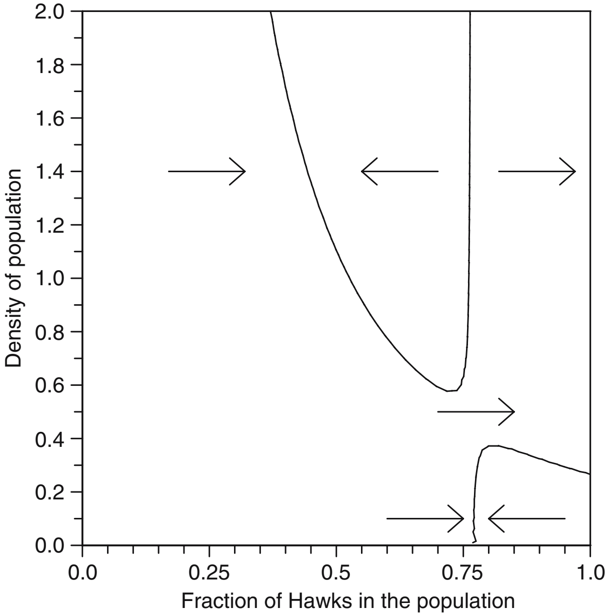

Fig. 6. Dependence of the dynamics on P in Hawk–Dove population, $t_a = 1.3$, $v_f f = 1$, $t_h = 5$, $v_h = 9$, $\alpha = 0.347$

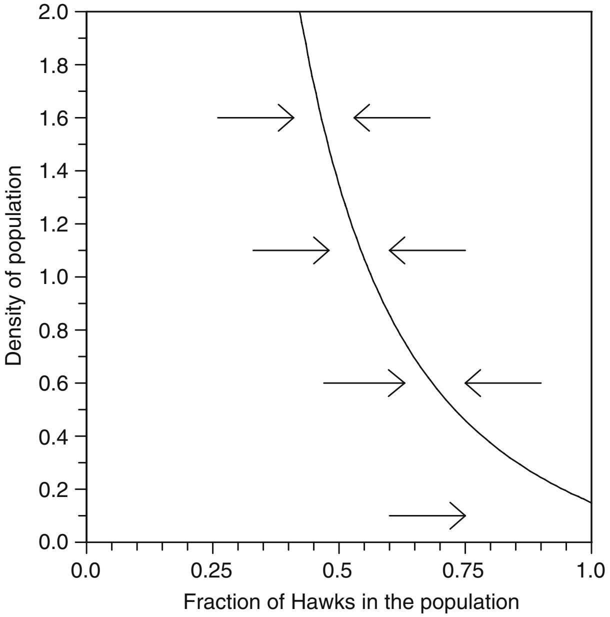

Fig. 7. Dependence of the dynamics on P in Hawk-Dove population, $t_a = 0.8$, $v_f f = 1$, $t_h = 5$, $v_h = 9$, $\alpha = 0.75$

The only cases where inner attracting points may occur are mixtures of Hawk–Doves and Marauder–Retaliators, i.e. cases where p and r are parametrized by linear functions $f(x) = x$ and $g(x) = x$ (or $f(x) = x$ and $g(x) = 1 - x$). In either case, $f''(x) = g''(x) = 0$, and thus we have

$$\begin{aligned} &\frac{\mathrm{d}^2}{\mathrm{d}x^2} T(f(x), g(x), f(x_0), g(x_0)) \\ &\quad = \frac{\partial^2 (T_{\mathrm{S}} + T_{\mathrm{H}})}{\partial p^2} f'(x)^2 + 2 \frac{\partial^2 (T_{\mathrm{S}} + T_{\mathrm{H}})}{\partial r \partial p} f'(x) g'(x) \\ &\qquad + \frac{\partial^2 (T_{\mathrm{S}} + T_{\mathrm{H}})}{\partial r^2} g'(x)^2 \end{aligned}$$

where the corresponding formulas for second derivatives of T_S and T_{H} can be derived from formulas (5), (6), (8) and (9) as follows:

$$\begin{aligned} &\frac{\partial^2 T_{\mathrm{S}}}{\partial r^2} = \frac{\partial^2 T_{\mathrm{S}}}{\partial r \partial p} = \frac{\partial^2 T_S}{\partial p \partial r} = 0 \\ &\frac{\partial^2 T_{\mathrm{S}}}{\partial p^2} = -2 \cdot \frac{v_{\mathrm{h}} H (1 - r_{\mathrm{p}}(1-\alpha))}{v_{\mathrm{f}} f + v_{\mathrm{h}} H p (1 - r_{\mathrm{p}}(1-\alpha))} \cdot \frac{\partial T_S}{\partial p} \\ &\frac{\partial^2 T_{\mathrm{H}}}{\partial p^2} = t_{\mathrm{h}} v_{\mathrm{h}} S p_{\mathrm{p}} (1 - r(1-\alpha)) \cdot \frac{\partial^2 T_S}{\partial p^2} \\ &\frac{\partial^2 T_{\mathrm{H}}}{\partial r \partial p} = \frac{\partial^2 T_{\mathrm{H}}}{\partial p \partial r} = -t_{\mathrm{h}} v_{\mathrm{h}} S p_{\mathrm{p}} (1-\alpha) \frac{\partial T_S}{\partial p} \\ &\frac{\partial^2 T_{\mathrm{H}}}{\partial r^2} = 0 \end{aligned}$$

These formulas were used for numerical calculations using Maple 10. The numerical results suggest that

$$\frac{\mathrm{d}^2}{\mathrm{d}x^2} T(f(x), g(x), f(x_0), g(x_0)) \,\big|_{x=x_0} > 0$$

for all attracting points x_0.

4.9. *ESS versus CSS*

A strategy Σ is an ESS when it cannot be invaded by a small number of mutant strategists, see [14]. In our notation, $T(x, x_0)$ means the time the x-strategists needs to consume a food item in a population where everybody else uses strategy x_0. Hence, a strategy x_0 is an ESS if and only if $T(\cdot, x_0)$ attains its absolute minimum in x_0, in other words,

$$T(x_0, x_0) < T(x, x_0), \qquad \text{for all } x \neq x_0.$$

ESS and CSS do not coincide in general as shown, for example, in [6]. In our model, ESS and CSS are different as well. For example, it was shown above that for high density populations, Hawk is a CSS in the mixture of Hawks-Doves if

$\alpha < 1/2$ and P is large. However it follows from our formulas that a population of pure Hawks can be invaded by Doves i.e. Hawk is not an ESS for $\alpha < 1/2$ and large P for some parameter combinations.

For high P and $\alpha < 1/2$ we have

$$\begin{aligned} T_S(1,1) &\approx \frac{(t_a/2)}{\alpha}, \\ T_H(1,1) &= t_\mathrm{h} + t_\mathrm{h} v_\mathrm{h} S \left[T_\mathrm{S}(1,1)\alpha + \frac{t_a}{2} \right], \\ &\approx t_\mathrm{h} + t_\mathrm{h} v_\mathrm{h} S t_a \end{aligned}$$

and

$$\begin{aligned} T_\mathrm{S}(0,1) &= \frac{1}{v_\mathrm{f} f}, \\ T_\mathrm{H}(0,1) &= t_\mathrm{h} + t_\mathrm{h} v_\mathrm{h} S \frac{1}{v_\mathrm{f} f}. \end{aligned}$$

Thus, Hawk is not an ESS if

$$t_a > \frac{1}{v_\mathrm{f} f}.$$

Note that this result is different to that of Broom et al. [5] where the possible invading strategies included Retaliator and Marauder as well as Dove, but is the original condition for not challenging from [3].

5. Discussion

In this paper we have explicitly considered for the first time kleptoparastic populations where individuals play mixed strategies, and the population strategy changes following the adaptive dynamic procedure of small increments in the direction of maximizing fitness.

The extension of adaptive dynamics to kleptoparasitism allows us to consider more flexible behaviour amongst our population than in previous works. We have provided the general framework for how to solve such problems, which involves the direct calculation of searching and handling times, as opposed to the simpler handling ratio, which was equivalent for the purposes of earlier models. We developed this with the application to individuals who can vary their behaviour only between two distinct types of strategy (which nevertheless can be mixed strategies). We have given the conditions for either of the “pure” solutions (i.e. always play one of the two distinct types) and sufficient but not necessary conditions for there to be a mixture of these two types. We have not ruled out multiple mixed CSSs or a mixed CSS when these sufficient conditions are not met in the general case, although we do not consider such an occurrence likely for our system.

This in turn leads us to a full analysis of all pairs of possibilities from the strategy class of pure behaviours introduced in [5]. Four of the six possibilities lead to results not qualitatively different from those of [5] in the sense that the same pure solutions can occur here as well (although significant analysis was required for the Hawk–Marauder case). There are distinct results in the other two cases, where the two types differ in both of their parameters (which would generally be the case for a combination of two randomly selected mixed strategies). For the Marauder–Retaliator case, Marauder is always a CSS and there can be either no other CSS, pure Retaliator as a CSS or a mixed CSS. For the Hawk–Dove case there is either a pure Hawk CSS or a mixed CSS, or both solutions simultaneously. The different types of solutions possible can clearly be seen by varying the population density P for various values of the other parameters. The Hawk–Dove case in particular yields quite complex and interesting behaviour. We considered both high and low density cases analytically, as well as looking at a range of densities in Figs. 1–7. The major difference to earlier work is the existence of mixed stable solutions.

It should be noted that in the above discussion we are assuming that the attracting points of our dynamics are indeed CSSs. We believe this to be true; this was certainly the case for all of our numerical calculations, where we were unable to find any branching points of the dynamics. If this was not true, and branching points were possible, the behaviour of our system would be even richer, with all of the above possibilities plus others as yet undiscovered.

One pertinent question, is how plausible is it to restrict the population to only a combination of two strategies. It was shown in [5], which considered a polymorphic population of individuals playing pure strategies, for example, that no mixture of individuals playing Hawk and individuals playing Dove was possible, due to invasion by one of Marauder and Retaliator. If we allowed a mixture of all strategies at once the analysis would get very complex, and one reason we restricted our working to combinations of two strategies only was to make the calculations feasible. However, we can conjecture about the likely results in this case. In [5] it was not possible to have a mixed strategy solution; this was as a result of all individuals being absolutely identical in their abilities. Although the strategies that individuals played were different (polymorphic mixtures of pure strategies rather than monomorphic players of mixed strategies) we believe that this result will also carry over to this case. In more recent work [13] non-challenging individuals were allowed to search for food at a higher rate than challengers, and this allowed polymorphic mixtures to occur. In the current case, even if small differences in abilities are allowed, then mixed CSSs will be possible in the unrestricted case. For instance, if individuals differ in fighting ability according to how frequently they fight (Hawk as opposed to Marauder or Retaliator) then our mixtures are possible even if individuals have a free choice. To illustrate it by an example, consider an extreme situation where any bird outside the Dove–Hawk diagonal has a zero chance of winning the fight. Such a bird can never invade a Hawk–Dove mixture because it does worse than Dove (that does not lose time fighting). In fact the outcome will be the same if birds playing strategies not on the diagonal have smaller fighting abilities (and thus smaller chances of winning the fight) than birds on the diagonal, even if these differences are small.

Another interesting question to consider is whether the strategies that we describe are actually used by real kleptoparasitic populations. The strategy Dove corresponds to populations where there is no kleptoparasitism, and the strategy

Hawk where there is widespread kleptoparasitism with visible contests, and so these two strategies are clearly common. A pure Retaliator population would be indistinguishable from a Dove one. Real populations that play Marauder would be characterised by frequent very short contests. Behaviour of this type often occurs in various wading birds [23], although this could be linked to dominance relationships between the birds. Mixed strategies have been observed in the common kestrel *Falco tinnunculus* [10] and its kleptoparasites (of various species). Birds take some opportunities to challenge but not all, and resist some challenges but not all. It should be noted that this is complicated by the different propensities of males and female to resist challenges, with females resisting challenges more often.

The use of adaptive dynamics provides a way to consider more complex interactions between individuals with different possibilities and could be useful for more complex kleptoparasitic populations with different types of individuals and behaviour. In this paper we have thus introduced an alternative method which is potentially very useful in tackling the important and challenging problem of kleptoparasitic behaviour.

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