The evolution of kleptoparasitism under adaptive dynamics without restrictions

by

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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. Strategic choices available to individuals are to attempt to steal or not, and to resist such stealing attempts or not. In this paper we consider the evolution of mixed strategies under adaptive dynamics. Depending on the various parameters, there are different possible outcomes to the dynamics. One such outcome is the pure strategy where individuals both challenge and resist at all opportunities (Hawk), and another is when they always challenge but never resist (Marauder). It is also possible that the population cycles with no attractor. However, no stable mixed strategy is possible. Further the basin of attraction of the Marauder strategy is generally small, perhaps indicating why it is rare in nature despite being commonly stable in kleptoparasitism models.

Keywords. kleptoparasite, food-stealing, game theory, strategy

1. INTRODUCTION

The phenomenon of kleptoparasitism, the stealing of food resources from conspecifics, frequently occurs within the context of intraspecific competition, notably amongst seabirds, [2]. Evolutionary game theory provides an ideal set of tools with which to examine this type of behavior. Such an approach has been the subject of several papers within recent years (eg [1, 3, 4, 5, 14, 15]). Most recently, Broom and Rychtář in [7] expanded on previous models of kleptoparasitism in monomorphic populations by allowing individuals to play mixed strategies and examining the dynamics which occur under incremental adaptation towards improved fitness. They considered only cases where strategies and the resultant adaptive dynamics were restricted to mixtures of two pure strategies. We consider a more general case, where we examine the adaptive dynamics which occur when any strategy is allowed. We show that in this case, no mixed strategy is stable and examine under what circumstances various pure strategies may be stable.

We follow the development in [7]. We consider a population, where, during the course of a search for food resources, an individual may encounter either a food item or a conspecific who has already obtained a food item, in which case the searcher may attempt to steal from the handler. In turn, the handler may either resist the attacker or surrender the food item and renew his own search. Each individual thus adopts a strategy $\Sigma = (p, r)$, where p is the probability that the individual will attack a handler and r is the probability that he will retaliate when attacked by a searcher.

1.1. **Model Parameters.**

We make use of the same parameters and variables as in [7]. The notation is summarized in Table 1.

We consider a population where the density of individuals is P. 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, handlers consume the food in an instant and resume searching.

Individuals are able to search an area ν_f for food in unit time. The number of available food items per unit area is given by f, so that the rate at which individual searchers find food is $\nu_f f$. The time to find a food item is thus drawn from an exponential distribution with mean $(\nu_f f)^{-1}$. Individuals also search for handlers, being able to search an area of size ν_h per unit time. Thus, the rate at which individual searchers find a handler is $\nu_h H$ and the time to find a handler is drawn from an exponential distribution with mean $(\nu_h H)^{-1}$.

When a searcher encounters a handler, it can challenge for the food item, or not. If it challenges, then the handler can resist, or not. If it resists, then a fight ensues (with times drawn from an exponential distribution with mean time $\frac{t_a}{2}$). At the end of a contest, the winner starts handling the food, and the loser resumes searching. The probability of the challenger winning the contest is given by α.

The individuals in the populations are engaged in three different activities - handling (H), searching (S), aggressive fighting (A) - the symbols for which will be used to represent both the activity and the density of individuals involved in that particular activity. The values of H, S, A can be determined from the previous parameters, see [7] for derivation of the formulae below.

$$P = S + H + A, \tag{1}$$

$$H = \nu_f f t_h S, \tag{2}$$

$$A = \nu_h H S p_P \ r_P t_a = H^2 t_a \nu_h p_P r_P / (\nu_f f t_h), \tag{3}$$

$$0 = H^2 t_a \nu_h p_P r_P + H(1 + \nu_f f t_h) - \nu_f f t_h P. \tag{4}$$

1.2. **Calculating fitness.** The time $T(\Sigma, \Sigma_P)$, the total time required for food procurement from the initiation of searching to the end of handling for an individual adopting strategy Σ in a population where all other individuals adopt strategy Σ_P, is taken as the sole indicator of individual fitness. The higher the time $T(\Sigma, \Sigma_P)$, the lower the fitness of the individual. Note that we regard time as the only currency in our model; in particular, the only cost of fights is their duration.

Following [7], we divide T into a searching period and a handling period. The schematic diagrams describing the periods are given on Figures 1 and 2. We write

$$T = T_S + T_H$$

where T_S is the time needed to acquire the food item, including possible fights, and T_H, is the time needed for the consumption of the food item, including possible fights and possible searching periods. It follows (see [7]) that

$$T_S = \frac{1 + \nu_h H p r_P \frac{t_a}{2}}{\nu_f f + \nu_h H p (1 - r_P(1-\alpha))}, \tag{5}$$

$$T_H = t_h + t_h \nu_h S p_P \Big[T_S (1 - r(1-\alpha)) + r \frac{t_a}{2} \Big]. \tag{6}$$

1.3. **Adaptive dynamics.** We shall consider the adaptive dynamics (see [7, 9, 10]) for the evolution of the trait Σ_P. The evolution favors changes in the direction of maximizing the fitness, i.e. minimizing the total time. Hence, the adaptive dynamics is given by

$$\frac{\mathrm{d}\Sigma_P}{\mathrm{d}t} = -\nabla_\Sigma T(\Sigma, \Sigma_P)\Big|_{\Sigma=\Sigma_P}. \tag{7}$$

The dynamics in components is

$$\frac{\mathrm{d}p_P}{\mathrm{d}t} = -\frac{\partial}{\partial p} T(p, r, p_P, r_P)\Big|_{p=p_P, r=r_P} = -\frac{\partial}{\partial p} T_S - \frac{\partial}{\partial p} T_H, \tag{8}$$

$$\frac{\mathrm{d}r_P}{\mathrm{d}t} = -\frac{\partial}{\partial r} T(p, r, p_P, r_P)\Big|_{p=p_P, r=r_P} = -\frac{\partial}{\partial r} T_S - \frac{\partial}{\partial r} T_H, \tag{9}$$

where, by (5), (6),

$$\frac{\partial T_S}{\partial p} = \frac{\nu_h H \Big\{ r_P \Big[\frac{t_a}{2} \nu_f f + (1-\alpha) \Big] - 1 \Big\}}{\Big(\nu_f f + \nu_h H p \big(1 - r_P(1-\alpha)\big) \Big)^2}, \tag{10}$$

$$\frac{\partial T_S}{\partial r} = 0, \tag{11}$$

$$\frac{\partial T_H}{\partial p} = t_h \nu_h S p_P \big(1 - r(1-\alpha)\big) \frac{\partial T_S}{\partial p}, \tag{12}$$

$$\frac{\partial T_H}{\partial r} = t_h \nu_h S p_P \Big[\frac{t_a}{2} - T_S (1-\alpha) \Big]. \tag{13}$$

For more on adaptive dynamics, see [8, 11, 12, 13].

Our goal is to analyze these dynamics. In particular, we want to find all (local) attractors. It follows from (10) and (12) that

$$-\frac{\partial T}{\partial p} \gtreqqless 0 \text{ if and only if } r_P \lesseqqgtr \frac{1}{\frac{t_a}{2}\nu_f f + (1-\alpha)}. \tag{14}$$

Hence, for small r_P, $-\frac{\partial T}{\partial p} > 0$ and thus the population evolves toward an increase in attacking probability. Moreover, if $\frac{t_a}{2}\nu_f f \le \alpha$, then $-\frac{\partial T}{\partial p} > 0$ for any $r_P \le 1$.

It follows from (11) and (13) that

$$-\frac{\partial T}{\partial r} \gtreqqless 0 \text{ if and only if } \frac{t_a}{2} - T_S(1-\alpha) \gtreqqless 0. \tag{15}$$

Due to the presence of T_S (which among other terms contains H as a function of r_P and p_P), the analysis of the above condition is not straightforward; in fact the behavior of $-\frac{\partial T}{\partial r}$ is more complicated than the behavior of $-\frac{\partial T}{\partial p}$, see Figures 5 and 6.

2. RESULTS

In the next sections we show that the only possible attractors of the dynamics are strategies $(p,r) = (1,1)$ and $(p,r) = (1,0)$. We will also investigate the bifurcation behavior on the line $\{(0,r); r \in [0,1]\}$.

2.1. **No inner strategy is an attractor.**

In this section we show that no inner strategy is an attractor of the dynamics. For a contradiction, assume that there is an inner attractor $\Sigma_0 = (p_0, r_0)$, $p_0, r_0 \in (0,1)$. Then,

$$-\nabla_\Sigma T(\Sigma, \Sigma_0)\Big|_{\Sigma=\Sigma_0} = 0.$$

As above, $\frac{\partial T}{\partial p} = 0$ if and only if

$$r_0 = \frac{1}{\nu_f f \frac{t_a}{2} + (1-\alpha)}; \tag{16}$$

and $\frac{\partial T}{\partial r} = 0$ if and only if

$$\frac{t_a}{2} - T_S(1-\alpha) = 0. \tag{17}$$

We consider two cases.

Case I. Assume $\nu_f f \frac{t_a}{2} \neq 1-\alpha$. Then, by (16), we have

$$2r_0(1-\alpha)-1 \neq 0$$

and from (5) and (17) we have

$$\frac{1+\nu_h H p_0 r_0 \frac{t_a}{2}}{\nu_f f + \nu_h H p_0[1-r_0(1-\alpha)]} = T_S = \frac{\frac{t_a}{2}}{1-\alpha}$$

which, using (16), simplifies to

$$\nu_h H \frac{t_a}{2} p_0[2r_0(1-\alpha)-1] = \nu_f f \frac{t_a}{2} - (1-\alpha) = -\frac{[2r_0(1-\alpha)-1]}{r_0}.$$

Thus, we get $p_0 = -\frac{1}{\nu_h H \frac{t_a}{2} r_0}$, which contradicts $p_0 > 0$.

Case II. If $\nu_f f \frac{t_a}{2} = 1-\alpha$, then, by (16), $r_0 = \frac{1}{2(1-\alpha)}$; and, by (5),

$$T_S(p,r,p_P,r_P) = \frac{1}{\nu_f f} \cdot \frac{\nu_f f + \nu_h H p r_P(1-\alpha)}{\nu_f f + \nu_h H p - \nu_h H p r_P(1-\alpha)}.$$

In particular, T_S is an increasing function of r_P and

$$T_S(p,r,p_P,r_0) = \frac{1}{\nu_f f}$$

for all $p, r \in [0,1]$. By the last equality and (13),

$$\frac{\partial T_H}{\partial r}(p,r,p_P,r_0)\Big|_{r=r_0} = 0$$

and consequently, all points (p_P, r_0) are steady points of the dynamics. But, these points are not attractors, since $\frac{\partial T_H}{\partial r}$ is a decreasing function of r_P, i.e. if the population has $r_P < r_0$, then r_P tends to be even smaller; and if the population has $r_P > r_0$, then r_P tends to be even larger.

2.2. **Conditions for a CSS on a boundary.** In this section, we will consider the behavior of the dynamics on the boundary. There are four "pure", or corner, strategies:

- Hawk - always challenge, always resist; $(p,r) = (1,1)$,
- Marauder - always challenge, never resist; $(p,r) = (1,0)$,
- Dove - never challenge, never resist; $(p,r) = (0,0)$,
- Retaliator - never challenge, always resist; $(p,r) = (0,1)$.

It was established in [7] that there are no attractors on the boundary between Dove and Marauder, Marauder and Hawk, Hawk and Retaliator. Clearly, all points on the line between Dove and Retaliator are steady points of the dynamics (and will be investigated later).

In this section we examine when Marauder and/or Hawk strategies are attractors.

2.2.1. *Marauder.* Marauder will be an attractor whenever

$$\frac{\partial T}{\partial p}\Big|_{p=p_P=1, r=r_P=0} < 0 \quad \text{and} \quad \frac{\partial T}{\partial r}\Big|_{p=p_P=1, r=r_P=0} > 0.$$

By (5),(10),(11),(12), and (13), this occurs whenever

$$\frac{t_a}{2}\nu_h H > (1-\alpha) - \frac{t_a}{2}\nu_f f, \tag{18}$$

where

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

following (4).

2.2.2. *Hawk.* Hawk will be an attractor whenever

$$\frac{\partial T}{\partial p}\Big|_{p=p_P=1, r=r_P=1} < 0 \quad \text{and} \quad \frac{\partial T}{\partial r}\Big|_{p=p_P=1, r=r_P=1} < 0.$$

By (5),(10),(11),(12), and (13), this occurs whenever

$$\frac{t_a}{2}\nu_f f < \alpha \tag{19}$$

$$\frac{t_a}{2}\nu_f f - (1-\alpha) < \nu_h H \frac{t_a}{2}(1-2\alpha) \tag{20}$$

where H solves (4).

2.2.3. *Dove.* As follows from the general analysis of the adaptive dynamics, we have $-\frac{\partial T}{\partial p}\Big|_{p=p_P=0, r=r_P=0} > 0$ and thus Dove is never CSS. In other words, in the population of Doves only, it is always beneficial to increase the probability of attacking.

Moreover, once the population is on the Dove-Retaliator line (i.e. in the state $\Sigma_P = (0, r_P)$, for any $r_P \in [0,1]$), then there are no fights and, by (5), (6),

$$T = \frac{1}{\nu_f f} + t_h$$

with $\frac{\partial T}{\partial r} = 0$.

2.2.4. *Retaliator.* Retaliator is never an attractor because, as with Dove, $\frac{\partial T}{\partial r} = 0$. On the other hand, unlike in the Dove case, the population can reach Retaliator through the evolution along the adaptive dynamics. For that, one needs

$$-\frac{\partial T}{\partial p}\Big|_{p=p_P=0, r=r_P=1} < 0 \quad \text{and} \quad -\frac{\partial T}{\partial r}\Big|_{p=p_P=0, r=r_P=1} > 0$$

for $0 < p = p_P \approx 0$ and $r = r_P = 1$. The above conditions are equivalent to

$$\frac{t_a}{2}\nu_f f > \alpha \quad \text{and} \quad \frac{t_a}{2}\nu_f f < (1-\alpha). \tag{21}$$

2.3. **Behavior on the Dove-Retaliator line.** In this section, we investigate the behavior on the Dove-Retaliator line. Since there are no fights in the population, the total time T does not depend on the probability of resisting an attack. Once the population reaches any point on this line, the population can become a polymorphic mixture of birds using any strategy $\Sigma = (0, r)$. Hence, it is not governed by the adaptive dynamics anymore.

The necessary condition for reaching the line is to have $-\frac{\partial T}{\partial p} < 0$ for some $p_P \approx 0$ and some r_P. Exactly as in the Retaliator case, this happens if and only if

$$r > r_0 = \frac{1}{\nu_f f \frac{t_a}{2} + (1-\alpha)},$$

i.e. if and only if

$$\frac{t_a}{2}\nu_f f > \alpha.$$

A population can leave the line as soon as the average probability to resist $\overline{r}$ is less then r_0, because then $\frac{\partial T}{\partial p} < 0$ in the "left" neighborhood of $(0, \overline{r})$.

Strictly speaking, a population can be polymorphic and the adaptive dynamics no longer rules its evolution. On the other hand, individuals can differ only in their resisting probability, and thus there are still no fights. For a potential invader of such a population, a polymorphic mixture of birds with average resistance $\overline{r}$ will have the same effect as a monomorphic population with $r_P = \overline{r}$. So we can still use the calculations we developed for the adaptive dynamics.

Since close to Dove ($r_P \approx 0$) one always has $\frac{\partial T}{\partial p} < 0$, the population can always leave the line.

Let us now investigate $\frac{\partial T}{\partial r}$. On the Dove-Retaliator line $\frac{\partial T}{\partial r} = 0$, i.e. there is no pressure to change the level of resistance and the population can freely drift along the line. But, by (5), for $0 \approx p = p_P > 0$, one has

$$T_S \approx \frac{1}{\nu_f f}$$

and thus, by (15), if $\frac{t_a}{2}\nu_f f < (1-\alpha)$ then there is a tendency to increase resistance (close to the Dove-Retaliator line).

The singular case $\frac{t_a}{2}\nu_f f = (1-\alpha)$ was already investigated (Section 3, Case II), and the results are that for $r_P < r_0$ there is a tendency to decrease resistance and for $r_P > r_0$ there is a tendency to increase it.

If $\frac{t_a}{2}\nu_f f > (1-\alpha)$ there is a tendency to decrease the resistance even further (see for example Figure 4). By (18), Marauder is a CSS and thus the population will eventually leave the Dove-Retaliator line permanently and end at Marauder.

Possible scenarios. There is the possibility of cycling behavior if

$$\frac{t_a}{2}\nu_f f > \alpha \quad \text{and} \quad \frac{t_a}{2}\nu_f f < (1-\alpha).$$

Under these conditions, the population can reach Retaliator. At this very moment, the population can become polymorphic. As soon as the average resistance falls below r_0, then fights appear and the population becomes monomorphic again. Due to the condition $\frac{t_a}{2}\nu_f f < (1-\alpha)$, the resistance will increase above the critical value r_0 and then the willingness to fight will start to fall as well. This is the case in Figure 6a.

Figure 6b depicts the same behavior and with the same parameters, with the exception that the density of the population is higher. Thus, Marauder emerges as another CSS. Although we do not have an analytical proof of this fact, numerical simulations suggest that once the population is around the Dove-Retaliator line, it will cycle forever and will never depart toward Marauder.

Figure 4 depicts behavior under the conditions

$$\frac{t_a}{2}\nu_f f > \alpha \quad \text{and} \quad \frac{t_a}{2}\nu_f f > (1-\alpha).$$

For such a set of parameters, the population can reach the Dove-Retaliator line and theoretically could stay somewhere around Retaliator drifting a little bit up and down. However, this is a highly unstable state since the population can drift along the line below the r_0 level and then will move permanently towards Marauder.

2.4. **Results summary.** There are three possible outcomes of the adaptive dynamics: Marauder is a CSS, Hawk is a CSS, or there is indefinite cycling through Retaliator. No other CSS, in particular a mixed CSS, is possible.

By (18), Marauder is a CSS whenever

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

Thus, Marauder is a CSS for any parameters provided P is large enough. Moreover, Marauder is a CSS (for any value of P) if

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

The condition means at least one of the following

M1) fights are long,

M2) there is enough food,

M3) a defender has only a small chance of winning a fight.

Hawk is a CSS if

$$\frac{t_a}{2}\nu_f f \quad < \quad \alpha \qquad \text{and} \tag{22}$$

$$\frac{t_a}{2}\nu_f f - (1-\alpha) \quad < \quad \nu_h H \frac{t_a}{2}(1-2\alpha). \tag{23}$$

The first condition says that it is better to attack if at least one of the following happens

H1) fights are not long,

H2) there is not enough food,

H3) an attacker has a big chance of winning a fight.

One can see that while H1 complements M1 and H2 complements M2, H3 and M3 are identical.

The cycling behavior occurs (and also Retaliator can be reached) if

$$\frac{t_a}{2}\nu_f f > \alpha \quad \text{and} \quad \frac{t_a}{2}\nu_f f < (1-\alpha).$$

Notice that the first condition is opposite to one of the conditions for Hawks. The two conditions hold together only if $\alpha < 1-\alpha$ and thus they mean that cycling occurs only if

C1) the chances of winning the fight as a defender are higher than the chances of winning the fight as an attacker,

C2) there is enough food in order to not attempt to steal it, but not enough to afford to not defend it.

3. DISCUSSION

We have investigated the adaptive dynamics for an unrestricted set of strategies of kleptoparasitic behavior. We have identified three possible outcomes of the adaptive dynamics: namely that Marauder is a CSS, Hawk is a CSS, or that there is indefinite cycling through Retaliator. There are no other CSSs of the dynamics. In particular, a mixed CSS is not possible.

Furthermore, these outcomes are not mutually exclusive because Marauder emerges as a CSS for any parameter values as long as P is high enough and can occur with either of the other two possibilities. However Hawk is never a CSS at the same time as the cycling behavior occurs.

The last and most interesting outcome of the dynamics is that the population can evolve in cycles going through Retaliator. This happens under the same conditions as for Retaliator being accessible. This cycling behavior involves going through periods of polymorphic mixtures on the Dove-Retaliator line and thus this behavior cannot be predicted for the following reasons. First, it is not clear how long the population will stay on the Dove-Retaliator line (specifically, how long it will take for a population to evolve by a drift to the state where the average resistance drops below the critical value r_0). Second, it is not clear where exactly the population leaves the Dove-Retaliator line (other than it has to be below r_0). Thus, the cycles may take a different amount of time and may be even of a different shape.

This paper brings new insights in the evolution of kleptoparasitic behavior. It provides a way to predict where the populations will end if it started in a known mixture. For example, we can see that Dove will evolve to Hawk rather than to Marauder although the rule in Dove populations is to increase the attacking probability leaving the resistance unchanged.

The paper may also explain why the Marauder strategy, despite being quite common in models of kleptoprasitism (see [5, 6, 7]), is not so commonly found in nature. Marauder emerges in all models for any parameter values whenever P is big enough. However, numerical simulations suggest that the region of attraction to Marauder is relatively small when Marauder emerges as a second CSS due to the high population density (see for example Figures 5b and 6b).

Furthermore, this paper also predicts the existence of cycling behavior, i.e. an evolution towards no particular attractor. This behavior was not captured by any of the preceding models. Each of the kleptoparasitism models starting with [3] considers behavior on a number of different timescales. 1) Short term changes in state (e.g. from handler to searcher) leading to convergence to equilibrium, which is typically a matter of minutes. 2) The contest between a resident population and a mutant to elimination or fixation of the mutant, which constitutes a small step in the adaptive dynamics of the population, strongly affected by the relative fitness of mutant and resident. This will typically take a significant number of generations to decide. 3) The time between the emergence of successive potentially viable mutations to compete with the resident population as in 2) above. It is assumed that this timescale is longer than that in 2). In this paper we describe a fourth, even longer timescale, where the speed of events is slower yet. This is drift along the Dove-Retaliator line, when there is no fitness advantage to aid either mutant or resident, and a succession of steps along the line following contests of type 2) and new mutations from 3) occur. This is central to the cycling behavior, which indicates this behavior happens very slowly indeed.

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Table 1

The model parameters and their definitions.

The top seven are the fundamental natural parameters, the next six terms represent the strategies played and the final terms are useful expressions which can be derived from the fundamental parameters and the strategies played

Symbol	Meaning
P	total density of individuals in the population
f	density of food items per unit area
ν_f	area that can be searched for food per unit time
ν_h	area that can be searched for handlers per unit time
t_h	expected handling time (if unchallenged)
$t_a/2$	expected duration of an aggressive contest
α	probability of the challenger winning the contest
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 $\Sigma_P = (p_P, r_P)$
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
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

Figure 1

Searching for a food item.

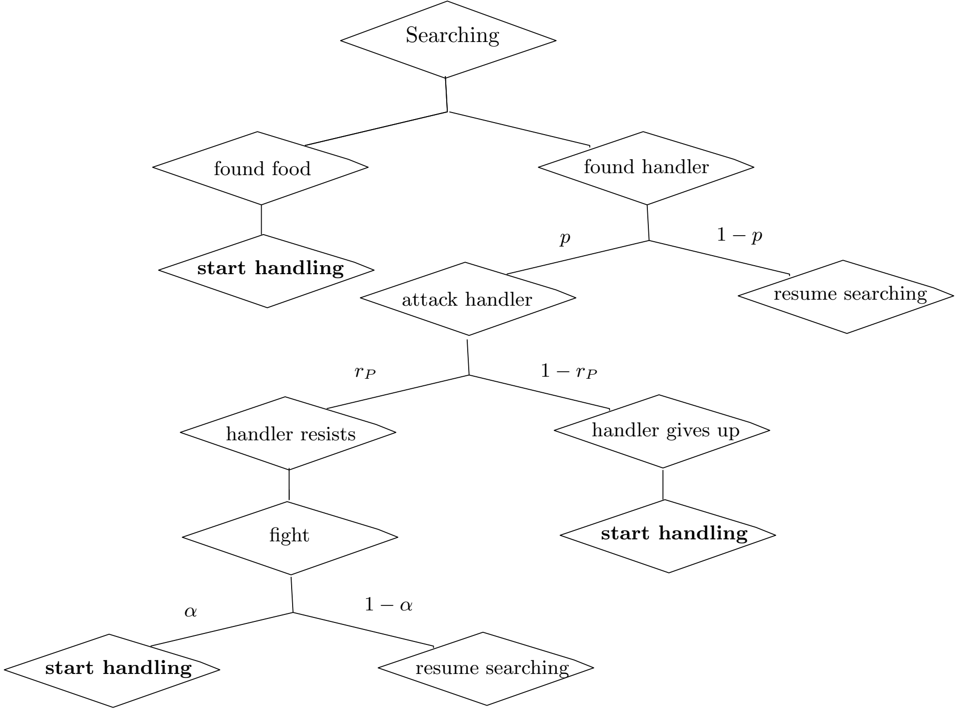


Figure 2

Handling a food item.

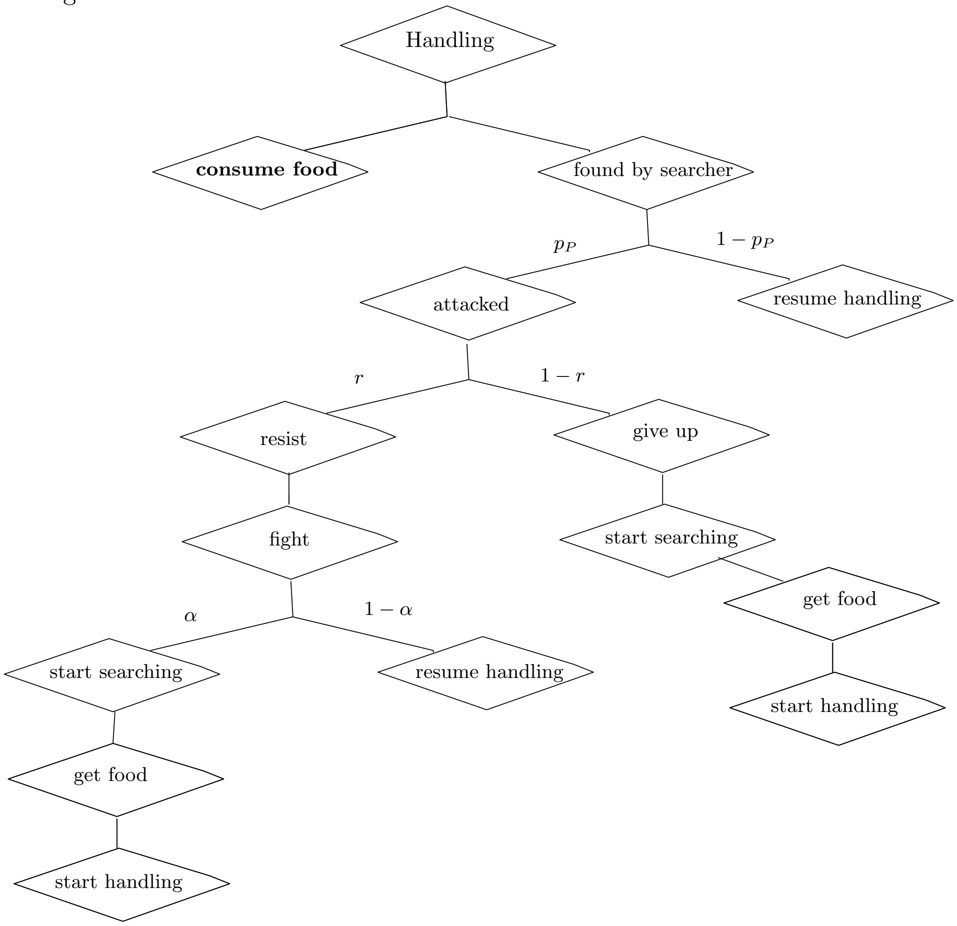


Figure 3

Adaptive dynamics in the case $\nu_f f \frac{t_a}{2} = 1 - \alpha$. In particular, parameter values are $t_a = 4/3, \nu_f f = 1, t_h = 2, \nu_h = 2, \alpha = 1/3, P = 3$.

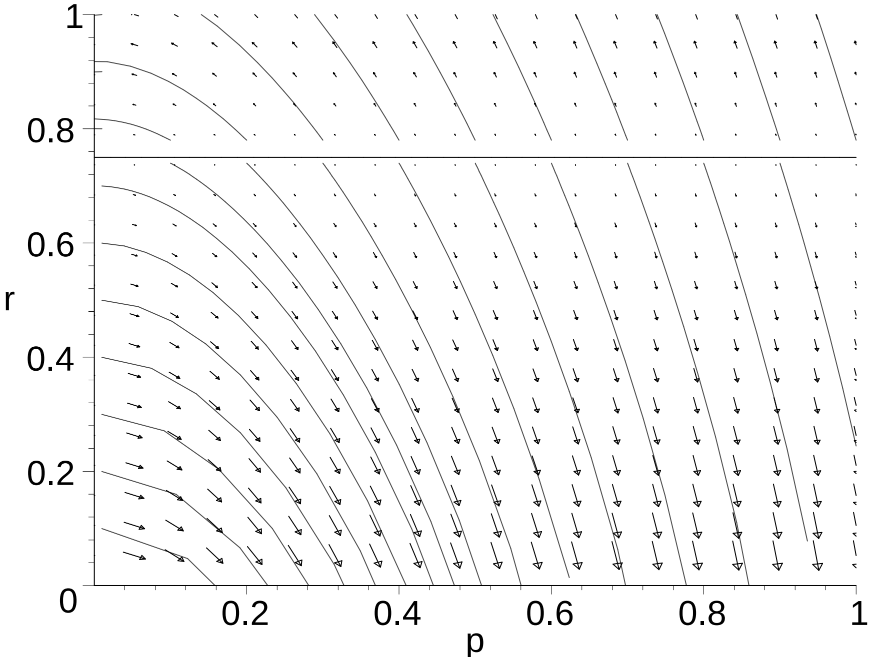


Figure 4

Marauder as an attractor. Parameter values are $t_a = 2, \nu_f f = 1, t_h = 1, \nu_h = 1, \alpha = 0.5, P = 1$. For this particular set of parameters, the population can reach Retaliator, but Retaliator is not stable.

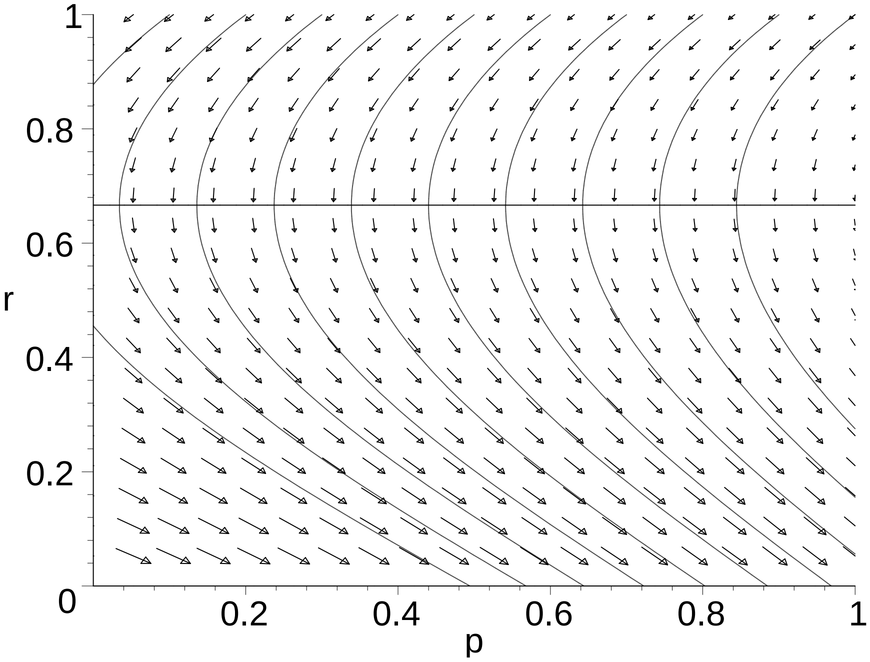


Figure 5

a) Hawk as an attractor. Parameter values are $t_a = 1, \nu_f f = 0.4, t_h = 1, \nu_h = 1, \alpha = 0.5, P = 1$; b) Marauder emerging as a second attractor together with Hawk, all parameters same but $P = 5$.

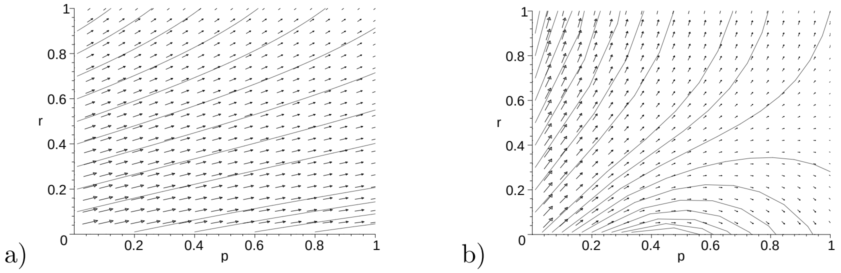
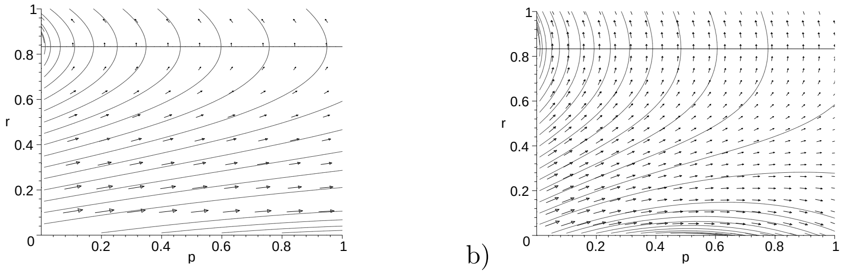


Figure 6

a) Cycling to Retaliator. Parameter values are $t_a = 2, \nu_f f = 0.5, t_h = 1, \nu_h = 0.5, \alpha = 0.3, P = 1$; b) Marauder emerging as an attractor; all parameters are as in a) except $P = 5$.



a)

b)