

# WHY DO FORAGERS FIGHT FOR FOOD? A UNIFYING EVOLUTIONARY PERSPECTIVE

WOUTER K. VAHL, G. SANDER VAN DOORN & FRANZ J. WEISSING

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## ABSTRACT

In many species, the intake rate of foraging individuals is negatively related to forager density due to agonistic interactions among foragers. Recently a variety of game theory models has been developed to address the question how such interference behaviour is shaped by natural selection. These modelling approaches have not yet led to a comprehensive understanding of interference competition; models that appear to be very similar yield strikingly different predictions regarding the evolutionary stability of various interference strategies. Here we attempt to unify approaches. To avoid model inconsistencies, we plead for a systematic, event-based description of the foraging process, the explicit account of feedback effects and the systematic derivation of a payoff function. To analyze the resulting evolutionary game, we use techniques from Adaptive Dynamics theory, since classical ESS techniques can be highly misleading when applied to the payoff functions resulting from interference competition. By means of this unified approach, we show that foraging animals can generally be expected to make their aggressive behaviour dependent on the role they play in interactions, that alternative evolutionarily stable interference strategies may evolve at the same ecological conditions, and that interference effects on intake rate cannot be taken for granted as the logical outcome of evolution. By critically discussing the setup, the assumptions and the way of analysis of some evolutionary models of interference competition, we identify crucial assumptions and potential pitfalls in modelling the evolution of interference behaviour, and we demonstrate that the discrepancies between earlier model predictions often reflect seemingly subtle differences in the assumptions on behavioural flexibility.

## INTRODUCTION

The intake rate of foraging animals is often negatively related to the density of foragers because of competition. Such negative effects can have major implications for the spatial distribution and population growth rates of both predators and their prey (Christian 1970; Gauthreaux 1978; Goss-Custard 1980). Competition is generally thought to arise in either of two ways (Keddy 2001). *Exploitative competition* is the negative effect of others through the removal of resources. As the exploitation of resources is a straightforward process, this type of competition is (presumably) relatively easy to understand. *Interference competition* is the negative effect of others through direct interactions between individuals. Behaviours underlying *interference competition* are various and complex (e.g., Huntingford & Turner 1987; Ens & Cayford 1996; Hassell 2000), and our understanding of this type of competition is still rudimentary (van der Meer & Ens 1997; Vahl et al. 2005a, b).

Several models have been developed to account for interference effects of forager density on foraging success. The original attempts have been reviewed by van der Meer and Ens (1997), who identified two broad approaches. Some ('phenomenological') models used an empirical relationship between foraging success and forager density to model the effect of interference, without further specification of the way interference competition comes about. Although such descriptive models may be useful for practical purposes, they yield little understanding of the interference process. Other ('mechanistic') models borrowed concepts from reaction kinetics to relate foraging success and forager density, assuming that interference competition arises from the loss of time spent in aggressive interactions. Such conceptual models seem a more promising approach to gain an understanding of the mechanistic basis of interference competition. This, however, is only partially the case, because these conceptual models do not consider the evolutionary question why foraging animals would interact with each other in the first place. The models assume foraging animals to interfere in a specific way without considering the adaptive value of such behaviour; as such, foraging animals are treated as 'aimless billiard balls' with no choice but to act aggressively when encountering each other (van der Meer & Ens 1997).

Recently, a variety of models has been developed that do consider the adaptive value of interference behaviour (e.g., Broom & Ruxton 1998; Sirot 2000; Dubois et al. 2003). The central question in these evolutionary models is how interference behaviour is shaped by natural selection. In addressing this question, these evolutionary models embed basic ideas from evolutionary game theory in a context that is based explicitly on a mechanistic description of animal foraging behaviour, using the mechanistic concepts from the original, non-adaptive models of interference competition. These evolutionary models extend pre-

vious work on evolutionary game theory (for reviews: see e.g., Maynard Smith 1982; Parker 1984; Hines 1987; Giraldeau & Livoreil 1998) by combining the study of frequency-dependent effects of aggressive behaviour with that of density-dependent ('interference') effects.

Although the number of evolutionary models of interference competition is growing rapidly, a comprehensive understanding of interference competition has not yet been achieved. Models that appear to be very similar yield strikingly different predictions regarding the evolutionary stability of various interference strategies. This is, for instance, clear from a comparison of those models of interference competition that (1) study the evolution of aggressive behaviour, (2) use the Hawk-Dove game, and (3) explicitly account for density-density dependent effects of foraging (for a short description of the most prominent of these models, see Table 6.1). These models address the same questions in similar ways. For instance, all of these models assume that foraging animals can be in a small number of mutually exclusive behavioural states, such as searching or handling, and they all predict how much foraging animals should behave aggressively in each of their behavioural states. Nevertheless, the models lead to strikingly different predictions regarding possible evolutionarily stable interference strategies, and regarding the effect of ecological variables on these predictions (Table 6.2). They vary, for instance, in their predictions on the nature and the number of evolutionary stable interference strategies, and there is no consensus on the effects of some prime ecological parameters. Regarding the effect of forager density, for instance, some models predict the frequency of aggressive conflicts to be high when the encounter rate with competitors is high, whereas other models predict few such conflicts, and yet other models predict the frequency of aggressive conflicts to be independent of the rate of competitor encounter.

This paper has a double purpose. We start by developing a systematic approach for studying the evolution of interference behaviour. This approach is event-based and centres on a decision tree that visualises the foraging game. For the analysis of the evolutionary stability of various interference behaviours, it relies on Adaptive Dynamics theory, which can be seen as a refinement of the methods of evolutionary game theory. With the help of this approach, we show that the degree to which a foraging animal behaves aggressively should reflect its behavioural state (i.e., whether it entered a conflict as a searcher or as a handler). We also demonstrate that at a substantial range of ecological conditions, interference strategies can be expected that do not result in a negative relationship between intake rate and forager density at all. The main purpose of the paper, however, is to discuss more critically the assumptions and pitfalls associated with modelling the evolution of interference behaviour. To this end, we discuss the models presented in Table 6.1 in the light of our systematic approach. We show that although these models have broadly the same struc-

**Table 6.1.** Description of models of interference behaviour that (1) study the evolution of aggressive behaviour, (2) use the Hawk-Dove game, and (3) explicitly account for density-dependent effects of foraging<sup>†</sup>

	special characteristics	sub-models
Broom & Ruxton 1998	use an event-based approach to evaluate different interference strategies; use a differential equation approach to study consequences of different strategies on the interference effect	<ol style="list-style-type: none"> <li>1. foragers search for food and for handlers concurrently (yes)</li> <li>2. trade-off between searching for food and searching for handlers (no)</li> </ol>
Broom & Ruxton 2003	extend Broom & Ruxton (1998); decision to behave aggressively is made dependent on the handling time invested by handling opponent	<ol style="list-style-type: none"> <li>1. 'apple model': food is consumed during handling (yes; model a)</li> <li>2. 'orange model': food is consumed after all handling has been done (yes; model b)</li> </ol>
Broom et al. 2004	upgrade Broom & Ruxton (1998) by allowing both searchers and handlers the choice to behave aggressively; use an approach that is mostly event-based	<ol style="list-style-type: none"> <li>1. searchers and handlers same probability of winning fights (yes; model a)</li> <li>2. searchers and handlers different probability of winning fights (yes; model b)</li> </ol>
Sirot 2000	uses an entirely event-based approach; keeps track of three types of prey items – those that are, those that will be, and those that will not be object of a conflict	
Dubois et al. 2003	consider effects of group size; forager density is assumed to affect interference behaviour only through effects on finder's advantage; do not keep track of number of foragers in each behavioural state	<ol style="list-style-type: none"> <li>1. only energy consequences considered (no)</li> <li>2. energy and time consequences considered (no)</li> <li>3. Hawk-Dove game with multiple challengers (yes)</li> </ol>
Dubois & Giraldeau 2003	iterated Hawk-Dove game in which foragers become familiar with their competitors; Hawk strategy is compared with Tit-for-Tat strategy	<ol style="list-style-type: none"> <li>1. payoff function evaluated is expected gain (yes)</li> <li>2. evaluates variance in expected gain (no)</li> <li>3. evaluates coefficient of variation of gain (no)</li> </ol>
Dubois & Giraldeau 2005	unite Hawk-Dove game with Producer-Scrounger game; incorporate predation risk for interfering foragers; do not keep track of number of foragers in each behavioural state	

<sup>†</sup> All of these models are based on the idea that foraging animals can be in few, mutually exclusive, behavioural states; indicated are only the special characteristics of the models. When a paper contained more than one model, sub-models are described and it is indicated whether we do (yes) or do not (no) consider them in our discussion of interference models.

**Table 6.2.** Predictions of evolutionary models of interference competition. Note that the models differ considerably in their predictions on whether specific interference strategies are expected to be evolutionarily stable, and on the effect of two of the prime model parameters – the rate at which unhandled food is found ( $\alpha x$ ) and the rate at which competitors are encountered ( $by$ ) – on the frequency with which foraging animals are expected to always behave aggressively (i.e., to play the Hawk strategy)

reference	ESS <sup>†</sup>						Alternative ESSs possible? <sup>‡</sup>	Parameter effects <sup>§</sup>	
	Dove	mixed	semi-mixed	Bourgeois	anti-Bourgeois	Hawk		$\alpha x$ $\uparrow$	$by$ $\uparrow$
Broom & Ruxton 1998	-	-	no	some	-	some	no	H $\downarrow$	0
Broom & Ruxton 2003	a	-	0	some	-	some	H&B	H $\downarrow$ , H $\downarrow$ $\uparrow$	H $\uparrow$
	b	-	0	some	-	some	no	H $\downarrow$	H $\downarrow$
Broom et al. 2004	a	0	0	no	some	some	H&X	0, H $\downarrow$	0, H $\downarrow$
	b	0	0	0	some	some	H&X, B&X	0, H $\downarrow$	0, H $\downarrow$
Sirot 2000	no	some	-	-	-	some	no	H $\downarrow$	H
Dubois et al. 2003	no	some	0	0	0	some	no	H $\downarrow$	H $\uparrow$ $\downarrow$
Dubois & Giraldeau 2003	no	-	-	-	-	some	no	H $\downarrow$	H
Dubois & Giraldeau 2005	no	no	some	no	no	some	no	H $\downarrow$	H

<sup>†</sup> Indicated is whether a strategy is excluded by explicit assumptions (-), ignored as a possible ESS (0), or predicted to occur under some conditions (some), or under no conditions (no).

<sup>‡</sup> Indicated is whether no alternative ESSs are predicted to occur under the same ecological conditions (no), or else, which of the Hawk (H), Bourgeois (B) and anti-Bourgeois (X) ESSs are predicted to co-occur under the same ecological conditions.

<sup>§</sup> Indicated is whether the frequency of the Hawk strategy is positively ( $\uparrow$ ), negatively ( $\downarrow$ ) or not (0) correlated to the rate at which unhandled food is found ( $\alpha x$ ) and the rate at which competitors are encountered ( $by$ ), or whether these relationships are concave ( $\updownarrow$ ) or convex ( $\downarrow\uparrow$ ). When alternative ESSs co-occur, multiple relationships are given.

ture, they differ substantially in the precise assumptions they make regarding, for instance, the structure of interactions, the presence of asymmetries and their payoff function. Such differences, although seemingly of minor importance, turn out to strongly affect predictions regarding the evolutionary stability of interference strategies.

## A MODELLING FRAMEWORK

### GENERAL OUTLINE

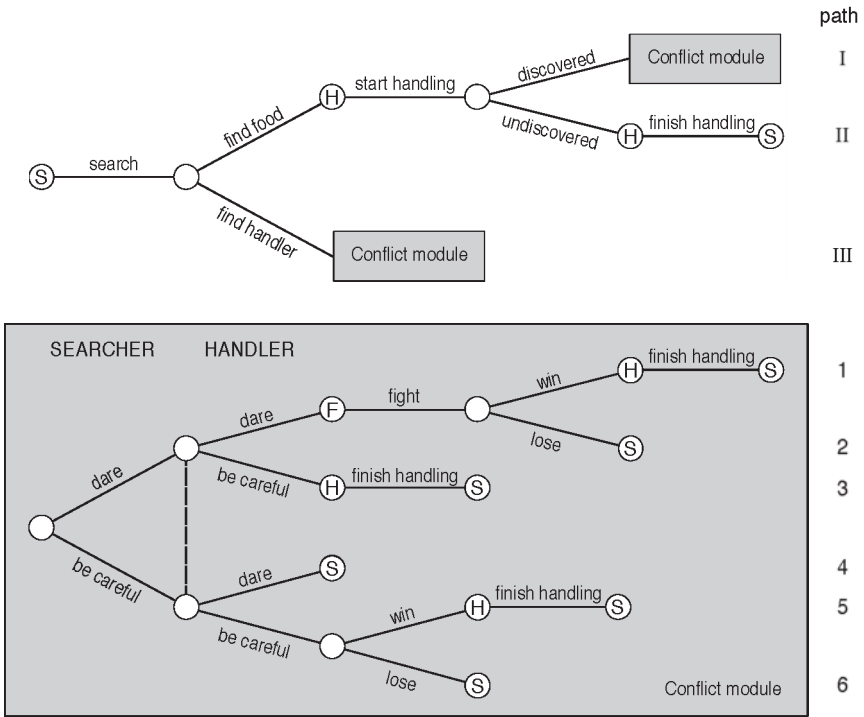
We consider a population of animals foraging in an environment that is determined by two main parameters: the density of food items  $x$  and the density of foragers  $y$ . We assume both food and foragers to be randomly distributed at constant density. This implies that food is not depleted and that the population of foragers is closed. Food items are assumed to be all alike, having a fixed energetic value to foragers, and requiring a fixed handling time. Foragers are assumed to be identical in all aspects other than their interference behaviour. At any moment in time, however, foragers may differ in the behavioural state they are in. Building on the approach of the original mechanistic models of interference competition (e.g., Beddington 1975; Ruxton et al. 1992), foraging animals are assumed to be in one of three, mutually exclusive, states: they can be *searching for*, *handling*, or *fighting over*, a food item.

To evaluate the behaviour of the foragers, we use an event-based approach; we consider a focal forager and keep track of the events that may happen to this forager, the actions that the forager can perform in response to these events, and the consequences of these actions to the behavioural state of the forager. In response to most events, a forager has no choice but to perform a specific action. Some events, however, create a choice situation; the action chosen in such a situation is determined by the forager's individual strategy. Each event and action has an expected consequence in terms of energy and time. For each sequence of events and actions, we can determine its probability of occurrence, as well as the energy and time consequences associated with it. Weighing consequences with probabilities, we get the payoff function associated with a strategy of the focal forager. This payoff function we use to evaluate the evolutionary stability of alternative strategies.

### MODEL STRUCTURE

#### EVENTS, ACTIONS AND STRATEGIES

To visualize the possible events, actions and strategic decisions, we use a decision tree (Figure 6.1). This tree starts with a focal forager that has just entered the searching state. Each chain of branches ends with the event or action that brings the focal forager back to the searching state. Two events can happen to



**Figure 6.1.** The foraging game visualized by a decision tree that keeps track of all possible events and actions that can occur to a focal forager. The decision tree starts with a forager in the searching state (S) and accordingly, each of the 13 paths through the decision tree end when the foragers re-enters the searching state. In the meantime, the forager may have been in the handling (H) and/or the fighting (F) state. The dotted line in the conflict module indicates that searchers and handlers choose an action simultaneously, without knowing the action of their opponent.

this searching forager. With probability  $\gamma$  it finds an unhandled food item, and with probability  $1 - \gamma$  it finds a competitor that is handling a food item. In the latter case, a conflict arises. In the former case the forager starts handling the food item and its behavioural state changes from searching to handling. When handling, again two events can happen to the forager: with probability  $\kappa$  it is discovered by a searching competitor and a conflict arises; with probability  $1 - \kappa$  the forager is not discovered. In the latter case the forager continues to handle its food item until it can be consumed; after consumption the forager re-enters the searching state. In the model discussed here,  $\kappa$  is implemented as a chance event. Alternatively, we could have treated it as a strategic decision; such would, for instance, have been appropriate in a producer-scrourer context.

When a conflict arises, the former searcher and the former handler both choose, simultaneously and independently, between two actions; they are either aggressive or not. In referring to these two behavioural options, we follow Crowley (2000); foragers either ‘dare’ or they ‘are careful’. The choice of either action is specified by their personal strategies  $P$ . Strategies have two components: the tendency  $p_s$  to ‘dare as a searcher’ and the tendency  $p_h$  to ‘dare as a handler’. If both opponents in a conflict choose to dare, they start a fight, with their state changing correspondingly. When fighting, two events can happen: with probability  $\alpha$  the searcher wins the fight, and with probability  $1 - \alpha$  the searcher loses the fight. If only one of the two opponents of a conflict dares, the daring forager wins the conflict and the careful forager loses it. If neither opponent dares, there is a peaceful contest, with both opponents having the same chance of winning. Winners take the food item and finish the handling of it, after which they re-enter the searching state. We assume that each food item is contested only once. This implies that handlers are certain not to be discovered while handling a food item that they have won in a contest. Losers re-enter the searching state. The conflict just described resembles the basic Hawk-Dove game with a role-asymmetry (Maynard-Smith & Parker 1976; Hammerstein 1981).

#### ENERGETIC CONSEQUENCES, TEMPORAL CONSEQUENCES AND PROBABILITIES

Only some actions have net energetic consequences (generically denoted by  $G$  for gain; for an overview of all symbols used: see Table 6.3). A handler that consumes a food item gains a constant amount of energy  $v$ ; it is assumed that food items are always consumed as a whole and instantaneously. A forager that enters the fighting state loses a constant amount of energy  $c$ . In the model developed here, we assume that there is no finder’s advantage, but such an advantage could easily be included in the model by assuming that a searcher that finds a food item gains a constant amount of energy  $d$  (in which case a handler that consumes a food item gains  $v - d$  instead of  $d$  energy units).

All actions bear a time consequence (generically denoted by  $T$  for time). We assume that foragers search simultaneously for unhandled food items and for food items that are being handled by a competitor, and that the discovery process of either type of food items is random. Under these assumptions, the expected time to find either a food item, or a handler  $t_s$  equals the inverse of the prey encounter rate, which is the sum of the rate  $\lambda_a$  at which unhandled food items are encountered and the rate  $\lambda_b$  at which food items owned by handlers are encountered:

$$t_s = \frac{1}{\lambda_a + \lambda_b} \quad [1]$$

The rate at which searchers encounter unhandled food items is a simple function of the constant rate  $a$  at which they search for unhandled food items and



**Table 6.3.** List of symbols used.

Symbol	Definition	Units
$a$	'Area of discovery of food': rate at which the environment is searched for food items	$\text{m}^2\text{s}^{-1}$
$b$	'Area of discovery of handlers': rate at which the environment is searched for handlers	$\text{m}^2\text{s}^{-1}$
$c$	Energy cost of each fight	J
$d$	Finder's advantage	J
$F_{p,\hat{p}}$	Invasion fitness of focal forager playing strategy $P$ in a population playing strategy $\hat{P}$	-
$G$	Expected energy consequence	J
$M$	Mutational variance-covariance matrix	-
$P$	Strategy, combining a value for $p_s$ and for $p_h$	-
$p_s$	Probability to dare as a searcher	-
$p_h$	Probability to dare as a handler	-
$T$	Expected time consequence	s
$t_f$	'Fighting time': expected time required to fight an opponent	s
$t_h$	'Handling time': expected time required to handle a food item before consumption	s
$t_{h1}$	'Initial handling time': expected time spent handling before discovery by competitor	s
$t_{h2}$	'Final handling time': expected time spent handling after discovery by competitor	s
$t_s$	'Searching time': expected time required to find either a food item or a handler	s
$v$	Energy value of each food item	J
$W_{p,\hat{p}}$	Payoff of focal forager playing strategy $P$ in a population playing strategy $\hat{P}$	$\text{J}\text{s}^{-1}$
$x$	Food density	$\#\text{m}^{-2}$
$y$	Forager density	$\#\text{m}^{-2}$
$\alpha$	Probability of winning when fighting	-
$\gamma$	Probability of finding a unhandled food item when searching	-
$\varepsilon$	Fraction of foragers with a mutant strategy	-
$\kappa$	Probability of being discovered when handling	-
$\lambda_a$	Rate at which searchers find unhandled food items	$\#\text{s}^{-1}$
$\lambda_b$	Rate at which searchers find food items owned by handlers	$\#\text{s}^{-1}$
$\lambda_s$	Rate at which a handler is discovered by searchers	$\#\text{s}^{-1}$
$\zeta_k$	Probability that focal forager achieves consequence $k$ ( $k = \text{'gain } v\text{'}, \text{'lose } c\text{'}, \text{ or 'spend } t_{h0}, t_{h1}, t_{h2} \text{ or } t_f\text{'}$ )	-
$\hat{p}_i$	Fraction of foragers in the population that are in state $i$ ( $i = \text{searching, handling or fighting}$ )	-
$\tau$	Evolutionary time	$\dagger$
$q_j$	Probability that focal forager passes the decision tree through path $j$ ( $j = 1 \dots n$ )	-

$\dagger$  The appropriate unit of evolutionary time depends on the rate at which mutations arise in the population. For instance, if mutation would create a single new mutant per generation, the unit of evolutionary time would correspond roughly to the generation time of the population under study.

the density of food items  $x$ :

$$\lambda_a = ax \tag{2}$$

The rate at which a handler is discovered by searchers is somewhat more complicated and will be specified below. The probability  $\gamma$  of a searcher finding an unhandled food item equals the proportion of food items found unhandled:

$$\gamma = \frac{\lambda_a}{\lambda_a + \lambda_b} \tag{3}$$

We assume that food items take a constant time  $t_h$  to handle. A forager that encountered an unhandled food item will thus spent  $t_h$  time handling when it is not discovered by a competitor. When it is discovered by a competitor, however, it will have spent part, but not all, of this time. Assuming that the discovery of handlers is a random process and that handler are discovered by searchers at a constant rate  $\lambda_s$  (which will be defined below), we take the probability  $\kappa$  of a handler being discovered by a searcher as one minus the null-term of the Poisson distribution:

$$\kappa = 1 - e^{-\lambda_s t_h} \tag{4}$$

Under the same assumptions, the expectation for the handling time invested before being discovered  $t_{h1}$  given that a handler is discovered equals the average waiting time of an exponential distribution divided by the probability  $\kappa$  of being discovered:

$$t_{h1} = \frac{1}{\kappa} \int_0^{t_h} t \lambda_s e^{-\lambda_s t} dt = \frac{1}{\kappa} [(1 - e^{-\lambda_s t_h}) \lambda_s - e^{-\lambda_s t_h} \lambda_s] = \lambda_s - \frac{1 - \kappa}{\kappa} t_h \tag{5}$$

The expected handling time left for the winner of a conflict  $t_{h2}$  is simply the difference between the total handling time  $t_h$  and the handling time invested prior to being discovered  $t_{h1}$ . This approach assumes that the total amount of handling time per food item is not affected by a conflict over this food item, and that there can only be one conflict per prey item.

We assume that fighting takes a constant time  $t_f$ . Conflicts in which at least one of the opponents chooses not to use aggression are assumed to be resolved instantaneously.

### THE PAYOFF FUNCTION

Knowing the expected consequences in terms of energy and time, as well as the probability of occurrence of each event and action, we can calculate for each strategy the expected payoff  $W_{P,\hat{P}}$ , whereby the notation indicates that the payoff is associated with a focal forager playing strategy  $P = (p_s, p_h)$  in a population of foragers that all play strategy  $\hat{P} = (\hat{p}_s, \hat{p}_h)$ . As payoff function, we use the ratio of the expected energy consequences over the expected time consequences (the 'long-term average rate of net energy gain'), which is one of the standard payoff functions used in models of foraging animals. In a subsequent

section (Section 4.4), we discuss the use of this specific currency in relation to its alternatives.

The long-term average rate of net energy gain equals the ratio of the sum of the energy consequences of each of the paths of the decision tree and the sum of the time consequences of each of the paths, whereby the energy consequences and the time consequences of each path  $j$  have to be weighted by the probability  $\varphi_j(P, \hat{P})$  of the focal forager passing through that path:

$$W_{P, \hat{P}} = \frac{E_{P, \hat{P}}(G)}{E_{P, \hat{P}}(T)} = \frac{\sum_{j=1}^n \varphi_j(P, \hat{P}) G_j}{\sum_{j=1}^n \varphi_j(P, \hat{P}) T_j} \quad [6]$$

Determining for each path the summed consequences in terms of energy and time is straightforward; the probabilities  $\varphi_j(P, \hat{P})$  of a focal forager taking path  $j$  through the decision tree can be found by multiplying the probabilities of all the events and actions in that path (Table 6.4). For ease of representation and interpretation, probabilities involving the same consequence in terms of energy or time can also be grouped into compound probabilities  $\zeta_k = \zeta_k(P, \hat{P})$  of reaching consequence  $k$ :

$$W_{P, \hat{P}} = \frac{\zeta_v v - \zeta_c c}{t_s + \zeta_{h_0} t_h + \zeta_{h_1} t_{h_1} + \zeta_{h_2} t_{h_2} + \zeta_f t_f} \quad [7]$$

Deriving the compound probabilities  $\zeta_k$  from the path frequencies  $\varphi_j$  as given in Table 6.4 is straightforward. The compound probability  $\zeta_c$  of losing  $c$  resources, for instance, is the sum of the probabilities  $\varphi_j$  of a focal forager taking each path that leads to the loss of  $c$  resources (i.e., the sum of the probabilities of the paths I-1, I-2, III-1 and III-2):

$$\zeta_v = \gamma \kappa [p_h \hat{p}_s \alpha + p_h (1 - \hat{p}_s) + (1 - p_h) (1 - \hat{p}_s) \alpha] + \gamma (1 - \kappa) + (1 - \gamma) [p_s \hat{p}_h \alpha + p_s (1 - \hat{p}_h) + (1 - p_s) (1 - \hat{p}_h) \alpha], \quad [8]$$

$$\zeta_c = \zeta_f = \gamma \kappa p_h \hat{p}_s + (1 - \gamma) p_s \hat{p}_h,$$

$$\zeta_{h_0} = \gamma (1 - \kappa),$$

$$\zeta_{h_1} = \gamma \kappa,$$

$$\zeta_{h_2} = \gamma \kappa [p_h \hat{p}_s \alpha + p_h (1 - \hat{p}_s) + (1 - p_h) (1 - \hat{p}_s) \alpha] + (1 - \gamma) [p_s \hat{p}_h \alpha + p_s (1 - \hat{p}_h) + (1 - p_s) (1 - \hat{p}_h) \alpha]$$

$$= \zeta_v - \gamma (1 - \kappa) = \zeta_v - \zeta_{h_0}.$$

**Table 6.4.** Summed consequences in terms of energy and time, associated with each of the paths of the decision tree, and the probability of a focal forager taking that path. Path numbers correspond to Figure 6.1.

Path ( $j$ )	Consequences		
	Energy ( $G_j$ )	Time ( $T_j$ )	Probability ( $\varphi_j$ )
I-1 find food, start handling, be discovered, dare, fight, win fight, finish handling	$v - c$	$t_s + t_{h_1} + t_f + t_{h_2}$	$\gamma \kappa p_h \hat{p}_s \alpha$
I-2 find food, start handling, be discovered, dare, fight, lose	$-c$	$t_s + t_{h_1} + t_f$	$\gamma \kappa p_h \hat{p}_s (1 - \alpha)$
I-3 find food, start handling, be discovered, dare, win conflict, finish handling	$v$	$t_s + t_{h_1} + t_{h_2}$	$\gamma \kappa p_h (1 - \hat{p}_s)$
I-4 find food, start handling, be discovered, be careful, lose conflict	$0$	$t_s + t_{h_1}$	$\gamma \kappa (1 - p_h) \hat{p}_s$
I-5 find food, start handling, be discovered, be careful, win peaceful contest, finish handling	$v$	$t_s + t_{h_1} + t_{h_2}$	$\gamma \kappa (1 - p_h) (1 - \hat{p}_s) \alpha$
I-6 find food, start handling, be discovered, be careful, lose peaceful contest	$0$	$t_s + t_{h_1}$	$\gamma \kappa (1 - p_h) (1 - \hat{p}_s) (1 - \alpha)$
II find food, start handling, be undiscovered, finish handling	$v$	$t_s + t_h$	$\gamma (1 - \kappa)$
III-1 find handler, dare, fight, win fight, finish handling	$v - c$	$t_s + t_f + t_{h_2}$	$(1 - \gamma) p_s \hat{p}_h \alpha$
III-2 find handler, dare, fight, lose fight	$-c$	$t_s + t_f$	$(1 - \gamma) p_s \hat{p}_h (1 - \alpha)$
III-3 find handler, dare, win conflict, finish handling	$v$	$t_s + t_{h_2}$	$(1 - \gamma) p_s (1 - \hat{p}_h)$
III-4 find handler, be careful, lose conflict	$0$	$t_s$	$(1 - \gamma) (1 - p_s) \hat{p}_h$
III-5 find handler, be careful, win peaceful contest, finish handling	$v$	$t_s + t_{h_2}$	$(1 - \gamma) (1 - p_s) (1 - \hat{p}_h) \alpha$
III-6 find handler, be careful, lose peaceful contest	$0$	$t_s$	$(1 - \gamma) (1 - p_s) (1 - \hat{p}_h) (1 - \alpha)$

When the focal forager plays the same strategy as the population, some of these compound probabilities can be simplified:

$$\hat{\xi}_v = \underbrace{\gamma(1-\kappa)}_{P(\text{no conflict})} + \underbrace{[1-\gamma(1-\kappa)]}_{P(\text{conflict})} \underbrace{[\hat{p}_s\hat{p}_h + (1-\hat{p}_s)(1-\hat{p}_h)]}_{P(\text{opponents same strategy})} \alpha + \underbrace{\gamma\kappa(1-\hat{p}_s)\hat{p}_h + (1-\gamma)\hat{p}_s(1-\hat{p}_h)}_{P(\text{only focal aggressive})} ,$$

$$\hat{\xi}_c = \hat{\xi}_f = \frac{[1-(1-\kappa)\gamma]}{P(\text{conflict})} \frac{\hat{p}_s\hat{p}_h}{P(\text{aggressive fight})} , \quad [9]$$

$$\hat{\xi}_{h_2} = \frac{[1-\gamma(1-\kappa)]}{P(\text{conflict})} \underbrace{[\hat{p}_s\hat{p}_h + (1-\hat{p}_s)(1-\hat{p}_h)]}_{P(\text{opponents same strategy})} \alpha + \frac{\gamma\kappa(1-\hat{p}_s)\hat{p}_h + (1-\gamma)\hat{p}_s(1-\hat{p}_h)}{P(\text{only focal aggressive})} .$$

#### FEEDBACK EFFECTS OF THE STRATEGY PLAYED BY THE POPULATION

At this point, we have fully specified the payoff function except for the rate  $\lambda_b$  at which searchers encounter food items owned by handlers and the rate  $\lambda_s$  at which handlers are discovered by searchers. Finding these two rates is somewhat complicated as both of them depend upon the fraction of foragers in one of the behavioural states; foragers will be more likely to find a food item owned by a handler when more foragers are in the handling state, and similarly, handlers will be more likely to be discovered when more of the foragers are searching. To account for this dependency, we have to keep track of the fraction of foragers  $\hat{\rho}_i = \rho_i(\hat{P})$  that is in each of the three states  $i$ , where the notation indicates that these fractions are assumed to depend on the strategy of the average individual in the population, but not on the strategy of the focal forager. Under this assumption, the rate  $\lambda_b$  at which searchers encounter food items owned by handlers is a simple function of the rate  $b$  at which they search for food items owned by handlers, the density of foragers  $y$ , and the fraction of foragers in the handling state  $\hat{\rho}_H$ :

$$\lambda_b = by(\hat{\rho}_{H_0} + \hat{\rho}_{H_1}). \quad [10]$$

This rate is independent of the fraction  $\hat{\rho}_{H_2}$  of foragers handling a food item that has been contested before, because we assume that food items can be the stake of a conflict only once. Similarly, the rate  $\lambda_s$  at which a handler is discovered by searchers equals the product of the rate  $b$  at which foragers search for food items owned by handlers, the density of foragers  $y$ , and the fraction of foragers in the searching state  $\hat{\rho}_s$ :

$$\lambda_s = by\hat{\rho}_s \quad [11]$$

Note that it is through the rates  $\lambda_b$  and  $\lambda_s$  that intake rate depends on the density of foragers.

What remains to be done is to determine the fractions  $\hat{\rho}_i$  of foragers in each of the three behavioural states  $i$ . At equilibrium, these fractions  $\hat{\rho}_i$  will equal the

relative amount of time that the average individual in the population of foragers spends in each of the behavioural states. Therefore, the fraction of foragers in each state follows naturally from the expectations on time allocation, which in turn follow from the compound probabilities  $\hat{\zeta}_k = \zeta_k(\hat{P})$  of reaching consequence  $k$  :

$$\hat{\rho}_s = \frac{E_{\hat{p},\hat{p}}(t_s)}{E_{\hat{p},\hat{p}}(T)} = \frac{t_s}{E_{\hat{p},\hat{p}}(T)} , \quad [12]$$

$$\hat{\rho}_{H_0} = \frac{E_{\hat{p},\hat{p}}(t_{h_0})}{E_{\hat{p},\hat{p}}(T)} = \frac{\hat{\zeta}_{h_0} t_{h_0}}{E_{\hat{p},\hat{p}}(T)} ,$$

$$\hat{\rho}_{H_1} = \frac{E_{\hat{p},\hat{p}}(t_{h_1})}{E_{\hat{p},\hat{p}}(T)} = \frac{\hat{\zeta}_{h_1} t_{h_1}}{E_{\hat{p},\hat{p}}(T)} ,$$

$$\hat{\rho}_{H_2} = \frac{E_{\hat{p},\hat{p}}(t_{h_2})}{E_{\hat{p},\hat{p}}(T)} = \frac{\hat{\zeta}_{h_2} t_{h_2}}{E_{\hat{p},\hat{p}}(T)} ,$$

$$\hat{\rho}_F = \frac{E_{\hat{p},\hat{p}}(t_f)}{E_{\hat{p},\hat{p}}(T)} = \frac{\hat{\zeta}_f t_f}{E_{\hat{p},\hat{p}}(T)} ,$$

The expected time consequences for the average individual in the population resembles the denominator of equation [7], but differs from it because the expected time consequences in equation [12] depend on the compound probabilities  $\hat{\zeta}_k$  of reaching consequence  $k$ , whereby the compound probabilities depend on the strategy played by the population, but not on the strategy played by the focal forager :

$$E_{\hat{p},\hat{p}}(T) = t_s + \hat{\zeta}_{h_0} t_{h_0} + \hat{\zeta}_{h_1} t_{h_1} + \hat{\zeta}_{h_2} t_{h_2} + \hat{\zeta}_f t_f . \quad [13]$$

### MODEL ANALYSIS

To analyze the evolutionary dynamics of interference behaviour we rely on techniques from *Adaptive Dynamics* theory (Dieckmann & Law 1996; Metz et al. 1996; Geritz et al. 1998; Hofbauer & Sigmund 1998; van Doorn et al. 2003a,b). According to this theory, the evolutionary rate of change of a strategy  $\hat{P}$  is given by the following dynamical equation (Dieckmann & Law 1996):

$$\frac{\partial \hat{P}}{\partial \tau} = M \left. \frac{\partial F_{p,\hat{p}}}{\partial P} \right|_{p=\hat{p}} , \quad [14]$$

where  $\tau$  is a measure of evolutionary time. Here,  $M$  is a *mutational variance-covariance matrix*, which, in our case, captures the genetic variance in the two strategic components ( $p_s$  and  $p_h$ ), and the covariance between them. The second

term on the right hand side of equation [14] is the *selection gradient*, which is the slope of the relationship between the fitness  $F_{p,\hat{p}}$  of a mutant playing strategy  $P = P(p_s, p_h)$  in a population of individuals playing strategy  $\hat{P} = P(\hat{p}_s, \hat{p}_h)$  and the mutant's strategy  $P$ , evaluated at the point where the mutant's strategy equals the strategy of the residents (i.e., where  $P = \hat{P}$ ). Here, the appropriate measure of fitness is the long term population growth rate of the mutant population in an environment set by the residents, that is, the *invasion fitness* (Metz et al. 1992; Rand et al. 1994). From equation [14] the full dynamics of evolving traits can be deduced. Evolution will end at *singular points* (Metz et al. 1996), where a change in evolutionary time does not result in a change in the trait value, that is, where equation [14] equals zero. The (invasion and convergence) stability of singular points can be deduced from the second order derivatives of the fitness function (e.g., Matessi & Pascuale 1996; Geritz et al. 1998; van Doorn et al. 2004).

### A SPECIFIC IMPLEMENTATION

The approach developed in the preceding paragraphs applies to models of the evolution of interference behaviour in general. In this section, we describe a specific implementation that we developed to illustrate the use of our approach by means of some predictions. In the next section we present these predictions.

As an approximation of invasion fitness, we used the payoff function associated with foraging. Given the complexity of our payoff function (i.e., equation [7]), we refrained from analysing the second order derivatives of our payoff function. Instead, we invoked numerical techniques to find the singular points of interference behaviour. In doing so, we restricted our attention to finding convergence stable endpoints of evolution, that is, endpoints that can be reached by evolution; the specific form of the payoff function used in our model ensures that convergence stable endpoints are also ESSs, that is, that they are stable against invasions (see Appendix).

To determine the convergence stable endpoints of evolution, we evaluated a grid of searcher and handler tendencies to dare (i.e., a grid of  $p_s$  and  $p_h$  values). For each combination of the strategic parameters in our grid, we studied the performance of mutants playing against a population of residents with that combination of strategic parameters. If the mutant did better than the resident, we adjusted the resident strategy in the direction of the mutant's strategy. For each of the points in our grid we repeated this procedure till the resident strategy converged to a stable endpoint. Practically, this was achieved by solving equation [14] for each point in our grid, using a standard algorithm for the numerical integration of ordinary differential equations; specifically, we used the 'odeint' Runge-Kutta driver with adaptive step size control as described in Press et al. (1992, p719). To exclude evolution towards equilibrium strategies that are sensitive to occasional errors in decision-making, we imposed all strate-

gic parameters to lie within the range  $[\delta, 1-\delta]$ , that is, we used the ‘trembling hand’ approach (Selten 1975). For all calculations we set  $\delta$  equal to  $10^{-6}$ . In our simulations, we used the following implementation of the mutational variance-covariance matrix:

$$M = \begin{bmatrix} 1 & 0 \\ 0 & 1 \end{bmatrix}, \tag{15}$$

assuming that both strategic components are fully subjected to natural selection (i.e., there is no constraint on the genetic variation in either component; the diagonal elements equal 1), and that the two strategic components evolve independent of each other (i.e., there is no covariance; the off-diagonal elements equal zero). The predictions presented below were all generated from a single set of parameters ( $c = 1$ ,  $t_f = 2$ ,  $t_h = 1$ ,  $v = 10$ , and  $\alpha = 1/2$ ).

## MODEL PREDICTIONS

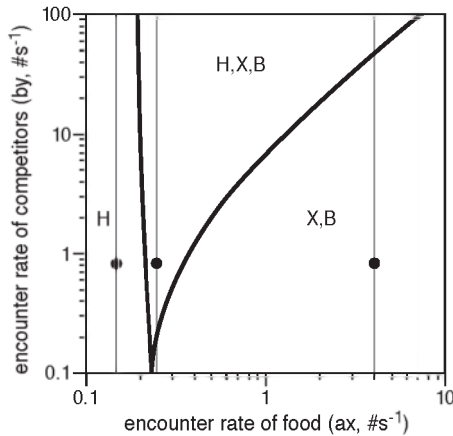
### EVOLUTIONARILY STABLE INTERFERENCE BEHAVIOUR

We find three evolutionarily stable interference strategies : 1) to always dare (i.e.  $p_s = 1, p_h = 1$ ), 2) to always be careful as a searcher and to always dare as a handler (i.e.  $p_s = 0, p_h = 1$ ), and 3) to always dare as a searcher and to always be careful as a handler (i.e.  $p_s = 1, p_h = 0$ ). Following Mesterton-Gibbons (1992), we refer to these three strategies as the Hawk, the Bourgeois and the anti-Bourgeois strategy, respectively. We do not find stable internal endpoints, and no endpoints on the boundaries of strategy space other than the three corner strategies mentioned above, meaning that no mixed strategy (‘to dare sometimes as a searcher, and to dare sometimes as a handler’) or semi-mixed strategy (‘to dare sometimes either as a searcher or as a handler’) is evolutionarily stable. Also, we do not find the *Dove* strategy (‘to always be careful’) to be evolutionarily stable. We do find that evolution can sometimes lead to alternative stable strategies. Which (combination) of the three evolutionarily stable interference strategies is reached depends on the rate of at which unhandled food is encountered and the rate of competitor encounter *by* (Figure 6.2).

When the rate at which unhandled food is encountered *ax* is low, the Hawk strategy evolves, regardless of the rate of competitor encounter *by* (Figure 6.2) and regardless of the strategic behaviour of the searchers and the handlers originally present in the population (Figure 6.3A). The Hawk strategy does best at this ecological condition because individuals that do not play the Hawk strategy save some time from fighting, but they do not find much food in this time saved from fighting, since the food encounter rate is low.

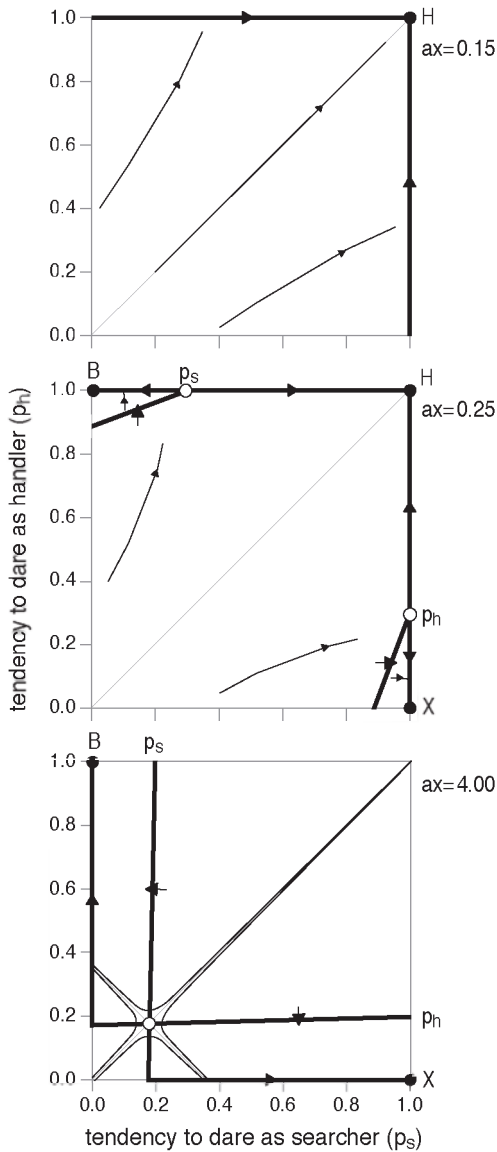
When the rate of food encounter is intermediate and the rate of competitor encounter is high, evolution can lead to all three of the evolutionarily stable





**Figure 6.2.** The outcome of evolution in relation to the rate at which unhandled food items are found ( $ax$ ) and the rate at which competitors are encountered ( $by$ ). Three regions are predicted that differ in the presence of the Hawk strategy (H), the anti-Bourgeois strategy (X) and the Bourgeois strategy (B) as potential outcomes of evolution. Symbols correspond to the parameter combinations of food encounter rate and competitor encounter rate used in Figure 6.3. Thin grey lines correspond to the food encounter rates for which the interference curves are given in Figure 6.4. Parameters values used:  $c = 1.00$ ,  $t_f = 2.00$ ,  $t_h = 1.00$ ,  $v = 10.00$ ,  $\alpha = 0.50$ .

interference strategies (Figure 6.2). Which of the three strategies is actually reached does not depend on the ecological conditions; rather, it depends on the strategies originally present in the population, and hence on the history of the population (Figure 6.3B). At most initial combinations of the two strategic components ( $p_s$  and  $p_h$ ) the Hawk strategy evolves. However, if the initial tendency to dare is high for searchers but low for handlers, or if the initial tendency to dare is low for searchers but high for handlers, evolution leads to the anti-Bourgeois and the Bourgeois strategy, respectively. That the Bourgeois and anti-Bourgeois strategies can be evolutionarily stable may come as a surprise. The Bourgeois strategy can be stable, because when the resident population plays the Bourgeois strategy, a mutant that sometimes dares as a searcher ( $p_s > 0$ ) is certain to gain resistance, and thus to lose time and energy to fights, whereas it will be certain not to lose time when finding food itself, given that a Bourgeois strategist never dares as a searcher. Similarly, when the resident population plays anti-Bourgeois, a mutant that sometimes dares as a handler ( $p_h > 0$ ) is certain to lose time and energy to fights, whereas the same individual will be certain not to lose time when it gives away its food item and dares some other individual that owns a food item, given that an anti-Bourgeois strategist never dares as a handler.



**Figure 6.3.** Trajectory plots showing how the tendency to dare as a searcher ( $p_s$ ) and as a handler ( $p_h$ ) evolve at low ( $ax = 0.15$ ), intermediate ( $ax = 0.25$ ), and high ( $ax = 4.00$ ) rates of food encounter ( $by = 0.80$ ,  $c = 1.00$ ,  $t_f = 2.00$ ,  $t_h = 1.00$ ,  $v = 10.00$ ,  $\alpha = 0.50$ ). Open and filled dots indicate unstable and stable singular points, respectively, whereby the letters indicate the Hawk strategy (H), the Bourgeois strategy (B), and the anti-Bourgeois strategy (X). Thick black lines are isolines for the tendency to dare as a searcher ( $p_s$ ) or as a handler ( $p_h$ ). Thin black lines are examples of evolutionary trajectories. Dotted lines are borders lines of different domains of attraction (separatrices).

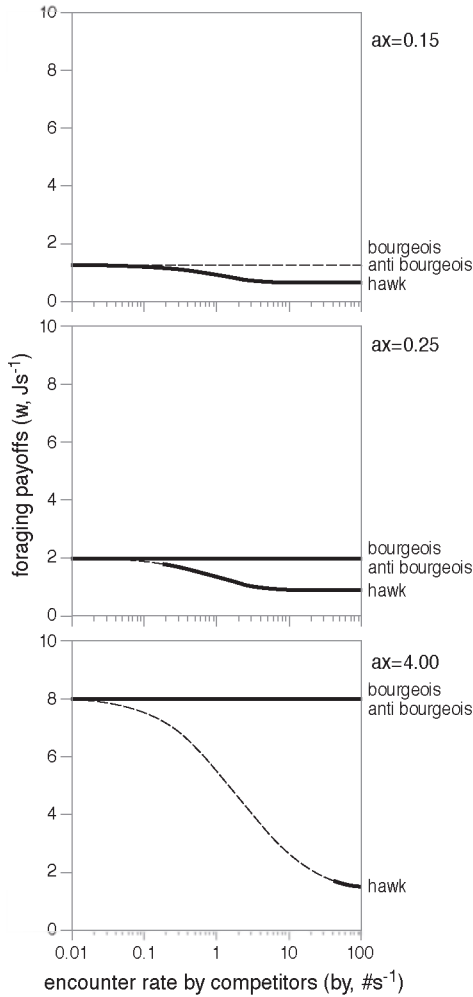
When the rate of food encounter is high and the rate of competitor encounter low or intermediate, evolution leads to either the anti-Bourgeois or the Bourgeois strategy (Figure 6.2): any population that starts with a higher tendency to dare as a searcher than to dare as a handler evolves to the anti-Bourgeois strategy, and all other populations evolve towards the Bourgeois strategy (Figure 6.3C). At these ecological conditions, the Hawk strategy is not evolutionarily stable. Apparently, the probability to find and consume food without being discovered is so high, that it does not pay to spend time and energy on fights.

### ECOLOGICAL CONSEQUENCES

Knowing the evolutionarily stable interference strategies, we can consider the interference effects that can be expected at the various ecological conditions. To do so, we study the relationship between the payoff of foraging and the rate at which competitors are encountered  $b$ , because we think that it is the combination of forager density  $y$  and the area of discovery of handlers  $b$ , rather than forager density per se, that matters.

When the rate at which unhandled food is encountered is low, only the Hawk strategy is evolutionarily stable (Figure 6.3A). In a population that plays the Hawk strategy, the payoff to foraging decreases with the rate at which competitors are encountered; at higher forager densities, more time is lost on fighting (Figure 6.4A). Even though the Bourgeois strategy and the anti-Bourgeois strategy will yield a higher payoff when played by all members of the population, playing Hawk is the best option for any individual; the Bourgeois strategy and the anti-Bourgeois strategy are not evolutionarily stable with respect to invasion by individuals that plays the Hawk strategy.

When the rate of food encounter is intermediate, the Bourgeois and the anti-Bourgeois strategy are the only stable strategies at low competitor encounter rates. At the higher competitor encounter rates, the Hawk strategy is also evolutionarily stable (Figure 6.3B). Interestingly, the payoff to foraging only decreases with forager density in populations that play the Hawk strategy; in populations that play the anti-Bourgeois strategy or the Bourgeois strategy no such interference effect is present (Figure 6.4B). The reason for this is that in populations that play the anti-Bourgeois strategy or the Bourgeois strategy overt fighting is absent. In a population that plays the Bourgeois strategy or the anti-Bourgeois strategy, non-aggressive conflicts (i.e., conflicts in which only one of the two opponents dares) do take place, but such conflicts are assumed to bear no costs. It is interesting to note that at the higher competitor encounter rates, populations in which all individuals play the Bourgeois strategy or the anti-Bourgeois strategy achieve a higher foraging payoff than populations in which individuals play the Hawk strategy. Nevertheless, the best strategy for an individual in the population where all individuals play the Hawk strategy still is to play the Hawk strategy itself.



**Figure 6.4.** Interference curves showing how the foraging payoff ( $W\hat{p}$ ) depends on the competitor encounter rate ( $b_y$ ) at low ( $ax = 0.15$ ), intermediate ( $ax = 0.25$ ), and high ( $ax = 4.00$ ) rates of food encounter ( $c = 1.00$ ,  $t_f = 2.00$ ,  $t_h = 1.00$ ,  $v = 10.00$ ,  $\alpha = 0.50$ ), for populations playing the Hawk strategy, the anti-Bourgeois strategy or the Bourgeois strategy. Solid and dotted lines indicate those parts of the interference curves for which the strategy played is and is not among the stable outcomes of evolution, respectively.

When the rate of food encounter is high, results are qualitatively the same as when the rate of food encounter is intermediate, but in populations that play the Hawk strategy the interference effect is much larger, and the Hawk strategy is only evolutionarily stable at high forager densities (Figure 6.4C).

## SOME GENERAL CONCLUSIONS

It was the main purpose of this paper to develop a conceptual contribution to modelling the evolution of interference behaviour. For that reason, we do not pretend to give a complete analysis of the model sketched above. Nevertheless, some general conclusions can be drawn regarding the evolutionary stability of interference strategies. First, we predict that evolution does not lead to the Dove strategy (to never dare); foraging animals will always be aggressive, either as a handler (Bourgeois strategy), or as a searcher (anti-Bourgeois strategy) or both as a searcher and as a handler (Hawk strategy). This prediction is not specific to the fact that foraging animals play the Hawk-Dove game repeatedly; given the presence of an asymmetry, the Hawk-Dove game generates the same predictions when it is played as a one-shot game (Maynard Smith 1982). Second, we predict that foraging animals in their role of searcher or handler will either always behave aggressively or never; we find no stable mixed strategies to evolve. When the encounter rate with unhandled food items is high, we do find an internal equilibrium point, but this is a saddle-point; the strategy to dare as a searcher evolves towards this equilibrium point, but the strategy to dare as a handler evolves away from it, so that evolution does not actually lead to this point. Third, we find that under certain ecological conditions, alternative interference strategies can be evolutionarily stable; which of the alternative strategies actually do evolve only depends on the interference strategies present at the start of evolution, and thus on the history of the population. This might explain why ecologically similar species or populations often differ strikingly in their behaviour towards conspecific foragers.

With regard to interference effects, we find that interference effects are only to be expected when populations play the Hawk strategy, that is, when foragers always behave aggressively. In populations that play the Bourgeois or the anti-Bourgeois strategy, intake rate is independent of forager density. These results imply that from an evolutionary perspective, interference effects cannot be taken for granted; at a substantial range of ecological conditions, foraging animals do not suffer from density-dependent effects. These predictions, however, should be interpreted with care, because they rely heavily on the assumption that conflicts in which only one of the opponents behaves aggressively bare no cost, neither in energy nor in time. Introducing a cost to losing a conflict in which only one of the two opponents dares may well make the evolution of the Bourgeois strategy and the anti-Bourgeois strategy less frequent, and it will introduce an interference effect to populations playing either of these two strategies. Although it seems unlikely that conflicts in which only one of the opponents behaves aggressively will be costly for the opponent winning such a conflict, the costs of such conflicts may be substantial for the opponent losing it, for instance, because it spends a considerable amount of time in running away from its opponent. Alternatively, it could be that interference competition

among foraging animals is mainly due to ‘non-adaptive’ interference effects, such as loss of concentration or loss of control over search paths.

## ASSUMPTIONS AND PITFALLS

In developing our approach, we have introduced a number of crucial ingredients that, according to us, should feature prominently in all models of the evolution of interference behaviour. These ingredients include (1) the structure of interactions, (2) the constraints that potentially arise through feedback effects of the strategy played by the majority of the foragers, (3) assumptions on asymmetries among foraging animals, (4) the precise form of the payoff function evaluated and (5) the techniques invoked to analyse the evolutionary stability of interference strategies. In this section, we determine how these features have been addressed by each of the models presented in Table 6.1, and where possible, we will relate these characteristics to the predictions generated by these models (Table 6.2).

### INTERACTION STRUCTURE

We find the basic structure of the various models to vary considerably (Table 6.5). To identify some of these differences, the decision tree proves very useful. Among others, the decision tree helps to reveal the consequences of constraints imposed deliberately by the various models (the ‘-’ signs). In the models of Dubois, for instance, it is assumed that foragers are always discovered when handling a food item (i.e., path II is excluded from their model). Similarly, Broom et al. (2004a,b) deliberately exclude the paths in which both opponents are careful (i.e., path 5 & 6 of the conflict module). Several of the models also constrain the strategic options of the foragers. Broom and Ruxton (1998, 2003a,b) assume that only searchers have the choice to act aggressively upon encountering a competitor; foragers that are discovered while handling a food item have no option but to respond aggressively to an encounter (i.e.,  $p_h = 1$ ). This assumption excludes three of the paths of the conflict module (Figure 6.1: path 3, 5 & 6). Dubois et al. (2003) assume that searchers only dare when their handling opponent does (i.e., path I-3 & I-4 are excluded). Sirot (2000) assumes that foragers apply the same aggressive strategy when in the searcher role as when in the handler role. These constraints on the foragers’ strategies implicitly introduce assumptions on the genetics underlying interference behaviour. Assuming that handlers have no choice but to behave aggressively, for instance, implies that there is no variation in the second strategic component. In terms of the mutational variance-covariance matrix this comes down to assuming the lower diagonal element to be zero. Assuming that the tendency to behave aggressively is independent of the behavioural state of foragers implies

**Table 6.5.** Classification of evolutionary models of interference competition according to our decision tree approach

reference	I						path <sup>†</sup>	III					
	1	2	3	4	5	6	II	1	2	3	4	5	6
Broom & Ruxton 1998	0	0	-	0	-	-	+	+	0	-	+	-	-
Broom & Ruxton 2003 a	0	0	-	0	-	-	0	+	+	-	0	-	-
	b	+	+	-	0	-	+	+	+	-	0	-	-
Broom et al. 2004	0	0	0	0	0	0	+	+	+	+	+	-	-
Sirot 2000	+	+	+	+	+	+	+	+	+	+	+	+	+
Dubois et al. 2003	+	+	-	-	+	‡	-	0	0	0	0	0	0
Dubois & Giraldeau 2003	+	+	+	-	+	‡	-	0	0	0	0	0	0
Dubois & Giraldeau 2005	+§		+	+		‡	-	+§		+	+		+‡

<sup>†</sup> Indicated is whether each of the paths of the decision tree is included (+), ignored (0) or excluded (-) by explicit assumptions (-). Latin numbers indicate whether foragers enter the conflict model after having found food themselves (I), after having found handlers (III), or do not enter the conflict model (II). Roman numbers indicate the six paths of the conflict model.

<sup>‡</sup> It is assumed that food items are shared among opponents, rather than that there is a peaceful contest between the opponents.

<sup>§</sup> It is assumed that food items are shared among opponents, rather than that there is a fight.

full covariance between the two strategic components (the off-diagonal elements of the variance-covariance matrix equal one). Although such constraints can in principle be defended as applying to specific systems, they generally are not defended as such; they more or less just slip into the models. To us, these assumptions seem unnecessary restrictive. Systematic characterisation of a decision tree will have the advantage that constraints imposed on the model have to be motivated explicitly.

Much more important, however, is the role of the decision tree with respect to constraints imposed implicitly on the model; in several models, one or more of the paths through the decision tree is not included in the payoff function (the '0's in Table 6.5). In all cases, the authors apparently are not aware that these aspects can play an important role in their model. In some models, this leads to major inconsistencies in the interaction structure. In the models of Broom and Ruxton (1998, 2003a,b), for instance, focal foragers in the searching state can find handlers to interact with (i.e., path III is included), but they themselves can not be detected by other searchers when handling a food item (i.e., path I is ignored). Similarly, while Dubois et al. (2003) and Dubois and Giraldeau (2003) assume that focal foragers handling a food item are always detected by other searchers (i.e., path I), the possibility that a focal searcher finds a food item owned by a handler (i.e., path III) is neglected.

## FEEDBACK EFFECTS

One of the crucial elements of the approach developed in Section 2 is that we explicitly acknowledge the presence of feedback effects; while the (aggressive) behaviour of a foraging animal depends on the role it plays in a conflict (i.e., searcher or handler), the probability of playing these roles in turn depends on the aggressive behaviour of other foragers, or more precisely, of the resident individuals. We find two such feedback effects. First, the rate  $\lambda_b$  at which searchers encounter food items owned by handlers depends on the fraction of foragers in the handling state. Second, the rate  $\lambda_s$  at which handlers are discovered by searchers depends on the fraction of foragers in the searching state. Indirectly, several other parameters are also affected by the behaviour played by the population. Both the expected time to find either a food item, or a handler  $t_s$  and the probability  $\gamma$  of a searcher finding an unhandled food item depend on  $\lambda_b$ . Similarly, both the probability  $\kappa$  of a handler being discovered by a searcher and the expected handling time invested before discovery  $t_{h_1}$  depend on  $\lambda_s$ . The reason why these feedback effects feature in evolutionary models of interactions among foraging animals, is that foraging animals interact repeatedly, and that the payoff functions of an interacting foragers depends on the summed outcome of several interactions. This creates the possibility of carryover effects through the fraction of foragers in each of the behavioural states. If each interaction could have been evaluated on itself, feedback effects would not have been an issue.

Several of the evolutionary models of interference competition do not acknowledge any of these feedback effects (Table 6.6); either ignoring them ('0's) or excluding them through explicit assumptions ('-' signs). Some of the other models do realise that  $\lambda_b$  and  $\lambda_s$  depend on the strategy played by the population, but they do not acknowledge that some of the other parameters are indirectly, through their dependency on either  $\lambda_b$  or  $\lambda_s$ , also affected by the population strategy. For instance, Sirot (2000) acknowledges that both the rate at which a handler is discovered by a searcher and the probability that this occurs, depends on the fraction of searchers. However, he does not account for the fact that the time spent handling before being discovered likewise depends on the fraction of searchers; rather he assumes that handlers are discovered after having spent half of the handling time.

Exclusion of any of the feedback effects seems unwanted because the presence of feedback effects can have far-reaching consequences for the outcome of evolutionary games. First, feedback effects can cause supposedly independent parameters to depend (implicitly) on the behaviour of the population of foraging animals. A more subtle, but potentially much more important effect of the feedback effects is that they can introduce non-linearities to payoff function that would otherwise have been linearly dependent on the strategies of both residents and mutants. Indeed, due to feedback effects through  $\lambda_b$  or  $\lambda_s$ , the payoff



**Table 6.6.** Feedback effects of strategy on various parameters of evolutionary models of interference competition.

reference	feedback effects <sup>†</sup>					
	$\lambda_b$	$\gamma$	$t_s$	$\lambda_s$	$\kappa$	$t_{t1}$
Broom & Ruxton 1998	0	0	0	0	0	0
Broom & Ruxton 2003	a	+	0	0	+	0
	b	+	+	+	+	+
Broom et al. 2004		+	+	+	0	0
Sirot 2000		+	+	0	+	+
Dubois et al. 2003		0	0	0	-	-
Dubois & Giraldeau 2003		0	0	0	-	-
Dubois & Giraldeau 2005		0	-	0	-	-

<sup>†</sup> Indicated is whether feedback effects of the strategy played by the population through each of six parameters are included (+), ignored (0) or excluded by explicit assumptions (-).

developed in Section 2 is a non-linear function of the strategy played by resident individuals. As much of evolutionary game theory was developed for linear matrix games, an important corollary of this is that insights from evolutionary game theory need no longer apply to the Hawk-Dove game when this is embedded in a foraging context. To give an example, it is a well-known theorem of evolutionary game theory that in the presence of asymmetries, no mixed strategies can evolve (Selten 1980). This theorem, however, was derived under the assumption of a bilinear payoff function (i.e., linear to both the strategy of mutants and the strategy of residents). Given that the payoff to foraging is a non-linear function of the interference strategy played by residents, this theorem cannot be invoked to exclude mixed strategies as possibly evolutionarily stable. In work on territorial animals, the presence or absence of feedback effects has indeed been shown to affect the occurrence of mixed strategies as potential outcomes of evolution. Eshel and Sansone (1995), for instance, who analyzed a Hawk-Dove game with a role-asymmetry, predicted no mixed ESS when feedback effects (of the strategy played by residents on the probability to find an empty territory and the probability to be discovered when owning a territory) were neglected, but semi-mixed ESSs, that is, strategies that were mixed in one of two components, when such feedback effects were acknowledged. Another subtle, but potential highly important consequence of feedback effects is that the choice of the payoff function may become much more important. In the presence of feedback effects, the usefulness of different currencies as approximations of invasion fitness depends strongly on the precise way feedback effects act upon the evolutionary game (Mylius & Dieckmann 1995).

## ASYMMETRIES

All models assume opponents in a conflict to differ in their role; foragers enter a conflict either as a searcher or as a handler. In most of the models, foragers are allowed to make their strategy dependent on this role; foragers have a separate tendency to dare as a searcher and as a handler (Table 6.7). Sirot (2000), however, does not allow for this role-asymmetry; interaction games in his model are symmetric, as he assumes foragers to have the same tendency to dare when entering a conflict as a searcher as when entering a conflict as a handler (i.e.,  $p_s = p_h$ ). By assuming this, Sirot reduces the strategy space subjected to evolution to a one-dimensional axis (corresponding to the positive diagonal of Figure 6.3), excluding the Bourgeois strategy, the anti-Bourgeois strategy and any semi-mixed strategy as potential outcomes of evolution. This difference between the model of Sirot (2000) and the other models is substantial; from classical evolutionary game theory it is well-known that the introduction of even the most minor asymmetries can drastically change the set evolutionarily stable strategies corresponding to a conflict (Maynard-Smith and Parker 1976; Hammerstein 1981). While the symmetric Hawk-Dove game, for instance, predicts a mixed strategy as a possible outcome of evolution, an evolutionarily stable strategy of an asymmetric Hawk-Dove game can only be obtained in pure strategies (Selten 1980). This might explain why Sirot (2000) predicts a mixed strategy to evolve, whereas no such strategy is predicted to evolve in the model developed in this paper; the stable mixed strategy of Sirot's symmetric game may well correspond to the unstable saddle-point found at the high food conditions in the asymmetric model developed in Section 3 (Figure 6.3C).

**Table 6.7.** Asymmetries assumed in models of the evolution of interference behaviour.

reference	role	asymmetry	
		RHP <sup>†</sup>	payoff <sup>†</sup>
Broom & Ruxton 1998	yes	0.5	0
Broom & Ruxton 2003	a	yes	$f(-)$
	b	yes	0
Broom et al. 2004	a	yes	0
	b	yes	$f(-)$
Sirot 2000	no	0.5	0
Dubois et al. 2003	yes	$f(\bar{a})$	$f(-)$
Dubois & Giraldeau 2003	yes	0.5	$f(se)$
Dubois & Giraldeau 2005	yes	0.5 <sup>‡</sup>	$f(-)$

<sup>†</sup> Indicated is whether the chance of winning a conflict ( $\alpha$ ) or the finder's advantage ( $d$ ) is specified, or variable ( $f(\cdot)$ ). In the latter case it is additionally indicated whether these parameters are a function of either the fighting ability ( $\bar{a}$ ) or the searching efficiency ( $se$ ) of the focal forager, or independent of any such characteristic (-).

<sup>‡</sup> The probability to win from another individual is fixed at 0.5, but as the number of contestants can exceed two and depends on the population strategy, the realized probability to win a fight is variable.

In addition to a role-asymmetry, several of the models allow the foragers to differ in either their resource holding potential (RHP), in the payoff associated with their behaviour, or in both these aspects. Broom et al. (2004b) and Dubois et al. (2003) introduce a RHP-asymmetry by allowing opponents to differ in their ability to win conflicts ( $\alpha$ ). Broom and Ruxton (2003a), in their 'apple model' introduce a payoff-asymmetry by assuming that handlers are certain to get a part of the food item proportional to the time they invest in handling. Similarly, in the models of Dubois, a payoff-asymmetry is introduced through the assumption of a finder's advantage  $d$ ; foragers that find a food item get at least a part of the resource, regardless of the outcome of the conflict. In the model of Dubois and Giraldeau (2003), the payoff-asymmetry is enhanced by individual differences in searching efficiency; efficient searchers receive the finder's advantage more often. All of these asymmetries elaborate the basic Hawk-Dove game; while the symmetrical game is a special case of the role-asymmetric game, games without difference in RHP or with no payoff-asymmetry are but special cases of the RHP-asymmetric and the payoff-asymmetric game, respectively. Introduction of different asymmetries, or different combinations of asymmetries may lead to radically different predictions (Eshel 2005), rendering the models incomparable.

### PAYOFF FUNCTION

All models use a short-term currency to approximate fitness. The general justification for this approach is to assume a positive relationship between intake rate and 'real' fitness. Although this assumption is common to most work on foraging animals (Stephens & Krebs 1986), the evidence supporting it is limited (but see Lemon 1991). Moreover, the generality of this assumption has been doubted (Maurer 1996). Moreover, the conditions that the relationship between intake rate and invasion fitness should fulfil in order for intake rate to be a useful approximation of invasion fitness are far from obvious. Determining these conditions, however, is a task on itself; here, we restrict ourselves to noting that a pure monotonous relationship does not guarantee that the same evolutionarily stable interference strategies are found when intake rate is used as when invasion fitness is used. Minimally, the relationship between intake and fitness should be linear (i.e.,  $F_{p,\hat{p}} \propto W_{p,\hat{p}}$ ).

The precise currency evaluated differs between the models (Table 6.8). Broom and Ruxton, in all their models, assume that there is no energetic cost to fighting (i.e.,  $c = 0$ ). Consequently, in most of their models they evaluate the expected time costs of interference behaviour; only in their apple model (Broom & Ruxton 2003a) they also consider the gains from fighting behaviour. These gains however, can easily be expressed in terms of time, given that there is a linear relationship between invested handling time and gain. Dubois and Giraldeau (2003) assume that both handling and fighting do not involve time

**Table 6.8.** Assumptions on the energy and time consequences and the currency evaluated in evolutionary models of interference competition.

reference	energy <sup>†</sup>		time <sup>†</sup>		currency
	<i>c</i>	<i>t<sub>h</sub></i>	<i>t<sub>f</sub></i>		
Broom & Ruxton 1998	0	$f(-)$	$f(-)$		$E(T)$
Broom & Ruxton 2003	a	0	$f(-)$	$f(-)$	$E(G/T)$
	b	0	$f(-)$	$f(-)$	$E(T)$
Broom et al. 2004	0	0 <sup>‡</sup>	$f(-)$		$E(T)$
Sirot 2000	$f(-)$	$f(-)$	$f(-)$		$E(G) / E(T)$
Dubois et al. 2003	0	0	$f(-)$		$E(G/T)$
Dubois & Giraldeau 2003	$f(-)$	0	0		$E(G)$
Dubois & Giraldeau 2005	$f(-)$	0	$f(-)$		$E(G/T)$

<sup>†</sup> Indicated is whether the energetic cost of fighting (*c*), the time cost of handling (*t<sub>h</sub>*), and the time cost of fighting (*t<sub>f</sub>*) are assumed to be constant (0), or variable and independent of any character ( $f(-)$ ).

<sup>‡</sup> Broom et al., (2004) assume the handling time of food items to be zero, but in deriving their model they rely on the results of Broom and Ruxton (1998), who assume handling to cost time, so that some of the findings of Broom et al. (2004) do depend on handling time.

costs (i.e.,  $t_h = 0$  and  $t_f = 0$ ). Consequently, they evaluate the expected net energy gain of interference behaviour. All other models consider the ratio of net energy gain and time, though in a subtly different way; while Broom and Ruxton (2003a), Dubois et al. (2003) and Dubois and Giraldeau (2005) consider the expectation of the ratio of net energy gain over time ('EoR': the expectation of the ratios), Sirot (2000) studies the ratio of the expectations of net energy gain and time (RoE: the ratio of expectations). The use of these two ratios has led to some ambiguity in the early literature on optimal foraging (see Stephens & Krebs 1986, Box 2.1), resulting from the fact that the average of a function is not necessarily equal to the function of the average (i.e.,  $E(G/T) \neq E(G)/E(T)$ ).

Which of these short-term currencies is to be preferred is not obvious. Use of either the expectation of the net energy gain or the expectation of the time costs seems restrictive as it assumes that either the time or the energy consequences are very small or absent. Regarding the two ratios: for biological reasons, it has been argued that the ratio of expectations (RoE) is to be preferred (Bateson & Kacelnik 1995; McNamara & Houston 1997), but the expectation of the ratio (EoR) can also be defended when the short-term performance of foraging animals is critical (Turelli et al. 1982; Stephens & Krebs 1986), or when the mental storage capacity of foragers is limited (Bateson & Kacelnik 1995). Both ratios, however, are rate-maximizing currencies, to which time constraints are implicit (Ydenberg et al. 1994). When foragers are unconstrained, or when they are constrained by energy rather than by time, currencies other than the

maximization of net energy gain rate may well be more realistic (e.g., Schmid-Hempel et al. 1985; Ydenberg et al. 1994; McNamara & Houston 1997).

### ANALYSIS

Most of the evolutionary models of interference competition use the classical approach to evolutionary game theory (Maynard-Smith 1982); they study the invasion stability of specific strategies by comparing the performance of different strategies when played against each other. In doing so, several of the models exclude certain strategies from analysis. Broom and Ruxton (1998, 2003a,b), for instance, by assuming that handlers always dare (i.e.,  $p_h = 1$ ), reduce the strategy space subjected to evolution to a one-dimensional axis (corresponding to the upper border in Figure 6.3). As a consequence, the Dove strategy, any mixed strategy and the anti-Bourgeois strategy are excluded from analysis.

Use of the classical approach would be appropriate for linear games, as in linear games invasion and convergence stability coincide. Due to the feedback effects of strategy on role, the payoff to foraging, however, is a non-linear function of the strategy played by residents. In non-linear games both the invasion and the convergence stability of singular strategies have to be studied, because invasion stable endpoints of evolution need not be attainable (Eshel 1983); in fact, any combination of invasion and convergence stability can occur (e.g., Geritz et al. 1998). The only study that determines whether singular points can actually be reached in the course of evolution, that is, whether they are convergence stable, is the study of Sirot (2000), who numerically evaluates the first order derivative of the payoff function. This implies that the evolutionarily stable interference strategies found by all other models may not actually be attainable in the course of evolution.

### CONCLUSIONS AND IMPLICATIONS

By applying our systematic approach to some evolutionary models of interference competition, we showed that modelling interference competition may not be as straightforward a task as it may appear to be at first sight. We found that specific events and actions were easily overseen, that feedback effects of the strategy played by residents on the role of focal foragers in conflicts were generally not accounted for, and that decisions regarding the payoff function used to evaluate the foraging game were often not made explicit. Proper account of these issues yields an approach to modelling the evolution of interference behaviour that is much more complete, but it also introduces the need for more sophisticated techniques of analyses than those generally used by evolutionary models of interference competition. Together, these improvements can drastically change ideas on the evolution of interference strategies.

## DIRECTIONS FOR FUTURE RESEARCH

A major assumption underlying our approach is the premise that the payoff to foraging with a certain strategy is linearly related to the invasion fitness of that strategy. Although similar assumptions underlie most work on foraging animals, such will be the case only under the most restrictive assumptions regarding the behaviour of the foraging animals and especially regarding the interaction between that behaviour and the environment (Mylius & Diekmann 1995). A more thorough derivation of the invasion fitness of a mutant strategy would, for instance, require explicit consideration of feedback effects of the strategy played by the animals on the dynamics of the foragers' prey. Although attempts have been made to reconcile game theory with explicit population dynamics (e.g., Rand et al. 1994), accounting for such feedback effects through the environment remains one of the major challenges for future research.

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## APPENDIX

The payoff function of the specific implementation of our framework that we consider in the main text (i.e., equation [7]) is a non-linear function of both the resident strategy and the mutant strategy. Due to its specific mathematical form, however, this payoff function behaves as if it were a linear function of the



mutant strategy. To see this, it is helpful to rephrase equation [7]:

$$W_{P,\hat{P}} = \frac{E(G)}{E(T)} = \frac{\zeta_v v - \zeta_c c}{t_s + \zeta_{h_0} t_h + \zeta_{h_1} t_{h_1} + \zeta_{h_2} t_{h_2} + \zeta_f t_f} = \frac{z_1 + z_2 P}{z_3 + z_4 P}, \quad [A1]$$

where  $z_1$  to  $z_4$  are parameters that depend on the resident strategy  $\hat{P}$ , but not on the mutant strategy  $P$ . From equation [A1] it is obvious that both the nominator and the denominator of the payoff function are linear functions of the mutant strategy  $P$ . As was pointed out by Sirot (2000), the interesting consequence of this linearity in both the nominator and the denominator is that the sign of the selection gradient (i.e., the first derivative of the payoff function with regard to the mutant strategy) is independent of the mutant strategy:

$$\frac{\partial W_{P,\hat{P}}}{\partial P} = \frac{z_1(z_3 + z_4 P) - (z_1 + z_2 P)z_4}{(z_3 + z_4 P)^2} = \frac{z_2 z_3 - z_1 z_4}{(z_3 + z_4 P)^2}. \quad [A2]$$

For a singular point to be invasion stable the second derivative of the payoff function to the mutant strategy should, in the neighbourhood of the singular point  $\tilde{P}$ , be less than zero:

$$\left. \frac{\partial^2 W_{P,\hat{P}}}{\partial^2 P} \right|_{P=\tilde{P}} < 0. \quad [A3]$$

For our payoff function this criterion is not met, as the second derivative of the payoff function to the mutant strategy equals zero, just as it does in the case of a payoff function that is a linear function of the mutant strategy. This implies that no singular point is invasion stable; at singular points all mutant strategies achieve the same payoff. For our analysis, this is not problematic, as convergence stable singular points will, in the long run, behave as if they were invasion stable. The reason for this is that any time a mutant succeeds to invade a population that is at a convergence stable singular point, natural selection ensures this population to converge back to the singular point.

From a mathematical point of view, the linearity of both the nominator and the denominator of the payoff function is a very special (if not trivial) case. In fact, it can be argued that all linear games are but degenerates of the more complete non-linear games (Rand et al., 1994). An important drawback of this is that the introduction of even the slightest non-linearity with regard to the mutant strategy in either the nominator or the denominator may qualitatively affect our results, for instance by creating the possibility of evolutionary branching (Geritz et al., 1998). Such non-linearities will, for instance, arise when paths through the decision tree contain more than one conflict; such would be the case if the assumption of at most one conflict per food item would be relaxed.

