UNIVERSITÉ DU QUÉBEC À MONTRÉAL

PROGRESS IN THE PRODUCER-SCROUNGER GAME: INFORMATION USE AND SPATIAL MODELS

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PROGRÈS DANS LE JEU PRODUCTEUR-CHAPARDEUR: L'UTILISATION DES INFORMATIONS ET DES MODÈLES SPATIAUX

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Dedicated to Brandy and Dawn.

One saw the end of this and one didn't,
but it wouldn't existed without both.

FOREWORD

In this doctoral thesis, five chapters are presented as scientific articles. The first article (Chapter II) was published in *Animal Behaviour* (Vol. 78, pp. 1343-1350) under the title "Finding the evolutionarily stable learning rule for frequency-dependent foraging". This article was co-authored by Steven Hamblin and Luc-Alain Giraldeau. Chapter III is an article published in *Oikos* (Vol. 119, pp. 286-291) entitled "Predator inadvertent social information use favors reduced clumping of its prey", and was co-authored by Steven Hamblin, Kimberley Mathot, Julie Morand-Ferron, Joseph Nocera, and Luc-Alain Giraldeau. In Chapter IV is the article "Scroungers are shy and producers are either: The co-evolution of boldness and foraging tactics", co-authored by Ralf Kurvers, Steven Hamblin, and Luc-Alain Giraldeau and submitted to the journal *Behavioral Ecology*. Chapter V contains the article "A rule of thumb for social foraging", co-authored by Steven Hamblin and Luc-Alain Giraldeau and submitted to *The American Naturalist*. Finally, Chapter VI is a single-author article by Steven Hamblin in preparation for journal submission (e.g. to *Proceedings of the Royal Academy, Series B* or Behavioral Ecology).

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It takes a village to raise a child.

African Proverb

My growth as a scientist has been shaped in both subtle and spectacular ways by many people; my successes are shared with them, but my failures are my own.

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Résumé

Les animaux grégaires en quête de ressources peuvent soit consacrer leurs efforts à la recherche (stratégie producteur) ou soit attendre que les producteurs réussissent à trouver ces ressources pour les y rejoindre (stratégie chapardeur). La profitabilité de chaque option peut être analysée par le jeu producteur-chapardeur. Ce jeu a été largement exploré aux plans théorique et empirique, mais plusieurs aspects demeurent toujours inexplorés. J'ai développé cinq modèles afin d'explorer l'approvisionnement social en lien avec l'utilisation d'information et les contraintes spatiales. Le premier modèle concerne l'évolution de règles d'apprentissage, des expressions mathématiques décrivant la valeur qu'un animal accorde aux options producteur et chapardeur en fonction des gains obtenus. J'ai démontré que la règle du *relative pay-off sum* est évolutivement stable et donc la meilleure disponible. Les paramètres de la règle attendue demeurent intrigants et demandent maintenant à être éplorés au niveau empirique. Le second modèle explorés plutôt l'effet de l'usage d'information sociale (chapardeur) chez un prédateur en examinant son effet sur l'évolution du niveau d'agrégation de ses proies. Le modèle démontre que les proies évoluent à différents niveaux d'agrégation en réponse à l'usage d'information sociale par leurs prédateurs et que cette relation affecte à la fois l'efficacité de recherche du prédateur et la survie des proies. Le troisième modèle teste l'hypothèse, générée à partir de recherche empirique sur les oies cendrées, selon laquelle la variation du niveau de hardiesse serait associée à un dimorphisme de producteurs hardis et de chapardeurs poltrons (*bold* et *shy*, respectivement) dans le jeu producteur-chapardeur. Le modèle réfute l'existence d'un tel dimorphisme, mais démontre néanmoins un effet environnemental fort des paramètres de l'approvisionnement social sur le niveau de hardiesse d'une population. Ce résultat a d'importantes implications pour le rôle de l'utilisation d'information et les effets spatiaux dans la régulation des relations entre les producteurs et les chapardeurs. J'ai développé à partir d'une approche d'automate cellulaire un modèle producteur-chapardeur pour déterminer si une règle simple (*rule of thumb*) fondée sur l'apprentissage social élémentaire dans un contexte spatialement explicite pouvait prédire l'atteinte d'un équilibre producteur chapardeur. Les résultats démontrent que l'ajout de cette règle simple génère à la fois une flexibilité comportementale significative et des dynamiques complexes qui ne sont pas habituelles à ce genre de systèmes simples. Le modèle lie l'usage d'information sociale à la structure spatiale dans un modèle déterministe. Enfin, avec le cinquième modèle j'ai exploré les effets de la géométrie du paysage (la façon dont l'espace est représenté, habituellement un quadrillage régulier) sur le jeu producteur-chapardeur. Il appert que les représentations spatiales sont un déterminant-clé dans la manière dont un jeu d'approvisionnement social d'alimentation peut réellement rendre compte de l'approvisionnement des animaux.

Key words: l'approvisionnement social, effets spatiaux, l'utilisation des informations, l'apprentissage, personnalités des animaux

Abstract

Animals foraging in groups can invest effort in searching for resources such as food (producing) or wait for producers to successfully find these resources and then join the discovery (scrounging); the game theoretical model that captures this situation is known as the producer-scrounger game. Producer-scrounger games have been well-studied theoretically and empirically, but a number of questions remain open. I created five models to explore new avenues in social foraging related to information use and the effects of spatial relationships. The first model tested the evolution of learning rules, mathematical descriptions of the value a foraging animal will place on the producing and scrounging tactics as a function of gathering personal information, to determine which candidate rule for foraging out of those previously published was most attractive in population dynamics. I found that one rule, the Relative Payoff Sum, was by far the most attractive and provided evidence that this rule is evolutionarily stable; the findings also pointed out intriguing features of parameter evolution amenable to empirical testing. The second model moves from personal to social information, examining predator-prey dynamics and the manipulation of information use in predators by prey as the outcome of a coevolutionary arms race. The model found that prey evolved different levels of clumping in response to predator use of social information (scrounging), and that this relationship affected both predator search efficiency and prey survival. The third model tested the hypothesis, generated from empirical work on geese, that the personality trait of boldness would create a dimorphism of bold producers and shy scroungers in a producer-scrounger game. This model failed to find such a dimorphism but did find strong environmental effects on the relationship between boldness and social foraging; this result has important implications for the role of information use and spatial effects in regulating producing and scrounging relationships. In the fourth model, I developed a cellular automaton producer-scrounger model to test the effect of a simple social learning 'rule of thumb' in a spatially explicit setting. The results show that adding this rule of thumb to the simplest possible producer-scrounger game generates significant behavioural flexibility and intricate population dynamics not usually seen in simple systems; the outcome of this model connects social information use to spatial structure among foragers in a deterministic and tractable model. Finally, in the fifth model I explored the effects of landscape geometry (the way in which space is represented, usually as a square grid) on the producer-scrounger game as part of a focused argument that spatial processes will be a key determinant in how this foraging game generalizes to real animal foraging.

Key words: social foraging, spatial effects, information use, learning, animal personality

CHAPTER I

GENERAL INTRODUCTION

> Social foraging theory offers a surprisingly rich, unexploited patch of untested models and predictions. May many readers discover and exploit it.
>
> *Giraldeau and Caraco (2000)*, p.334.

Producer-scrounger models have been a backbone of the study of social foraging, and the goal of this thesis is to add additional threads to the tapestry of theory and models woven around that framework. Three themes appear in what follows: additions to social foraging models, personal and social information use including learning, and spatial processes in foraging. To that end, in this introduction I will provide an overview of important background material for the chapters of the thesis, separated into five sections. In section I.1, I discuss the history and concepts of frequency dependent modelling of social foraging behaviours (social foraging theory and producer-scrounger games in particular). In section I.2, I discuss information use, both personal, and social, and the mechanisms of using such information to learn optimal behaviour as they apply to foraging models. Following that, in section I.3, I inspect the existing work on producer scrounger games in a spatially explicit world. In section I.4, I review the simulation methodologies that were used during this thesis and provide an introduction to each. Finally, in section I.5, I present an overview of the chapters and their relationship to each other, with attention paid to the fundamental thematic elements.

I.1 Frequency dependent ('social') foraging

When studying the evolution of animal foraging behaviour, two separate approaches have been taken throughout the years. The first, optimal foraging theory (Stephens and Krebs 1986; Stephens et al. 2007), focuses on economically 'optimal' decision making when individuals forage on their own; for example, when different prey types are presented sequentially, which types should be part of the optimal diet (the so-called 'prey model'; Stephens and Krebs 1986)? Optimal foraging theory can be used to predict aspects of foraging behaviour whether individuals forage as solitary individuals or as part of a group, but breaks down when group foragers receive payoffs as a function of the actions of other group members. This payoff relationship is studied by the application of game theory to foraging situations; the body of models and theory that has sprung up as a result is known as 'social foraging theory' (Giraldeau and Livoreil 1998; Giraldeau and Caraco 2000; Giraldeau and Dubois 2008).

I.1.1 Evolutionary game theory

A review of simple evolutionary game theory concepts is useful here, though it will be necessarily brief; Maynard Smith (1982) provides an excellent and accessible introduction to evolutionary game theory in general, and Giraldeau and Caraco (2000) is the seminal text on the application of these concepts to interdependent group foragers. (Note that 'evolutionary game theory' is also used to describe population dynamics concepts such as replicator dynamics. In the interest of concision, I will not deal with those more advanced topics here, but Hammerstein (1998) provides a useful overview).

Game theory is the study of optimal behaviour when an individual's best action depends on the actions of other individuals. A well-known example of this in animal behaviour is the case of animal aggression, as captured by Maynard Smith and Price (1973). Maynard Smith and Price took their motivating question to be 'why are animal fights so rarely fatal?', and the answer to that question came in the form of the Hawk-Dove model. In the model, two animals engage in an aggressive confrontation over a resource with a value V and each animal has two potential strategies. The first, Hawk, is an aggressive strategy, and the second, Dove, is a 'peaceful' strategy. If two Hawks meet, the result is an escalated conflict with a cost to losing C, such that each player receives a payoff of $(V - C)/2$ (divided by two because it is assumed that one Hawk loses 50% of the encounters and vice versa). If a Hawk meets a Dove, the Hawk takes the resource and the Dove escapes without injury, resulting in payoffs of V to the Hawk and 0 to the Dove. If two Doves meet, one or the other takes the resource with probability .5, so the resulting payoff is $V/2$. The variables and payoffs are summarized in Figure I.1.

		Player 2	
		Hawk	Dove
Player 1	Hawk	$(V - C)/2, (V - C)/2$	V,0
	Dove	0, V	$V/2, V/2$

Figure I.1: The Hawk-Dove game

Given this, what is the optimal strategy for each player? Passing over the mathematical details, it turns out that the Hawk-Dove game has a solution that takes the form of an *evolutionarily stable strategy* (hereafter ESS). Simply put, an ESS is a strategy which, when played by the whole population, cannot be invaded by a mutant playing a different strategy (Maynard Smith 1982). For example, as demonstrated in Maynard Smith and Price (1973), the Hawk-Dove game in Figure I.1 has an ESS wherein each player plays Hawk some times and Dove others (a 'mixed strategy'). The proportion of Hawk that each player should play turns out to be the ratio of the value of the resource to the cost of injury (V/C); thus, if $V = 20$ and $C = 30$, each player should play Hawk 2/3 of the time and Dove 1/3 of the time. This proportion of $\{2/3, 1/3\}$ is an ESS, because any mutant entering the population who played a different proportion of Hawk and Dove would do worse. The major contribution of the ESS concept to evolutionary biology arises from the linkage of natural selection to game theory, because in the example above mutants playing a different strategy will be selected out due to their reduced fitness, and thus natural selection will maintain the population at the ESS value. However, it is important to be aware that selection will maintain a population at an ESS (*stability*), but it may not take a population to that ESS point in the first place (*attractivity*; Hamblin and Hurd 2007; 2009). This is the subject of some discussion in Chapters II and V, though the issue can be ignored for games as simple as Hawk-Dove (see next section).

I.1.2 Frequency dependent selection

The process of selection which will lead a population to the mixed ESS in the Hawk-Dove game is known as frequency dependent selection, where the fitness of a phenotype is dependent on the frequency of that phenotype relative to the other phenotypes in the population (a notion adapted from population genetics: Maynard Smith 1982; Rice 2004). In negative frequency dependent selection (I will ignore the positive variant), phenotypes are more fit when they are rare, leading to a mixed ESS produced by selective pressures. This process is illustrated for a fictional situation in Figure I.2, where selection operates to adjust the population composition to the equilibrium point; if the population begins with mostly tactic 1 players, the frequency of tactic 1 players will decrease to the equilibrium point, while a population of mostly tactic 2 players will change in the opposite direction. The equilibrium will occur at the point where the fitnesses of the two tactics are equal. This is equivalent - for infinite populations - to saying that all individuals in the population adopt the same mixed strategy at equilibrium (a monomorphic population playing a mixed strategy instead of a polymorphic population playing pure strategies).

I.1.3 Evolutionary and ecological time

To this point, I have described evolutionary game theory and frequency dependent selection as envisioned by Maynard Smith (1982). The ESS concept adopted in this view is an explicitly genetic one; natural selection operates on individuals over generations to produce a population at equilibrium and maintain it at ESS frequencies. However, it is possible to consider frequency dependent selection without positing a specific underlying mechanism. When we do, the ESS solution concept is replaced by the more agnostic *stable equilibrium frequency* (SEF; Mottley and Giraldeau 2000; Giraldeau and Dubois 2008). Extending further, we can investigate how animals might solve game theory problems such as Hawk-Dove over ecological time (i.e. a period of time no longer than the individual's lifetime). A solution concept with an explicit behavioural mechanism has been labelled a behaviourally stable solution (BSS: Dawkins 1976; Giraldeau and Dubois 2008, Dawkins actually termed it a 'Developmentally Stable Strategy' or DSS, but I will follow modern usage and use BSS).

In the final chapter of his book, Maynard Smith (1982) suggested learning as a mechanism for BSSs, based in part on the work of Harley (1981) who published the

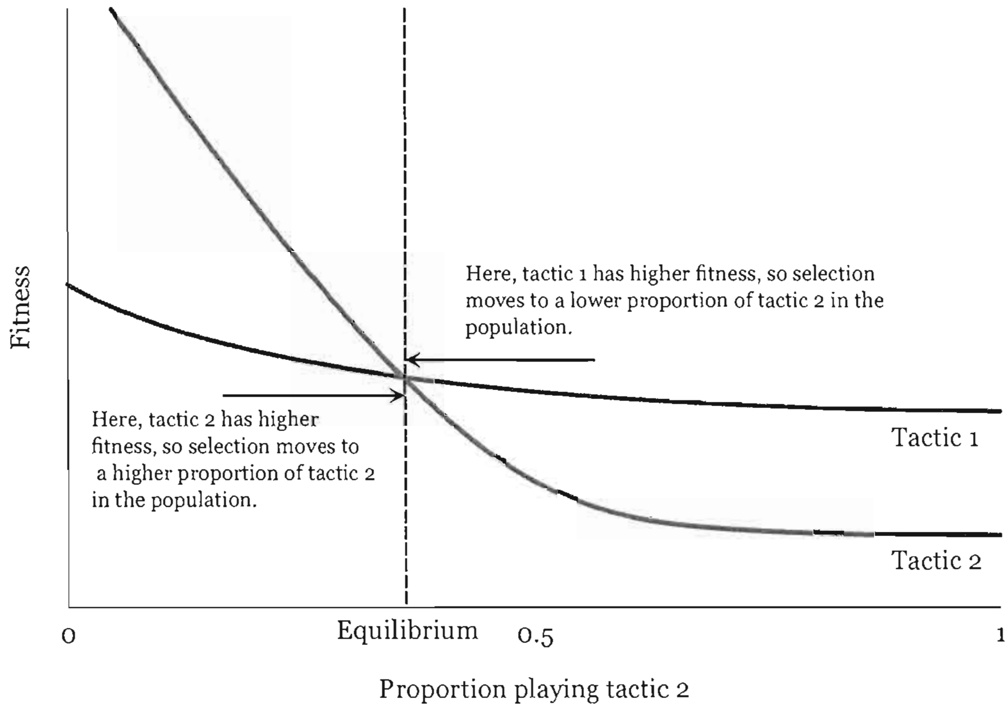

Figure I.2: Frequency dependent selection. Each tactic has greater fitness when it is rare, leading selection to move the population to a mixture of the two tactics where their fitnesses are equal (a mixed strategy, shown by the vertical line).

first attempt at providing such a mechanism. Harley coined the term 'evolutionarily stable learning rule' (ES learning rule) as part of an attempt to show that the BSS as achieved by an ES learning rule is the same outcome as the ESS (p.612):

> I will define the [B]SS as the strategy which is adopted by individuals with the evolutionarily stable (ES) learning rule. The ES learning rule is one such that all mutant individuals differing only in their learning rule will have a lower than average fitness when considered among a population of individuals who possess the ES learning rule. In other words, the ES learning rule is uninvadable. With some simplifying assumptions, it can be shown that the [B]SS for each game is in fact the ESS: the ES learning rule will cause a population to adopt the strategy which would be uninvadable if it were genetically determined.

I offer Table I.1 to summarize the solution concepts and clear any terminological fog.

Concept	Mechanism	Origin
ESS	Genetic	Maynard Smith (1972)
BSS	Behavioural (e.g. ES Learning rule)	Dawkins (1976)
SEF	None Implied	Mottley and Giraldeau (2000)

Table I.1: Summary of solution concepts.

Harley's initial proof was flawed (Harley 1983; Houston 1983; Houston and Sumida 1987; Harley 1987), but was later rescued (Tracy and Seaman Jr. 1995), and the search for mechanisms underlying BSSs remains an active area of research (recent review in McNamara and Houston 2009).

I.1.4 Social foraging models

The application of the tools outlined in the previous sections to the evolution of animal foraging behaviour resulted in the class of models that are collectively known as *social foraging theory* (Giraldeau and Caraco 2000). Of these models, arguably the most well-studied is the producer-scrounger game, first outlined by Barnard and Sibly (1981). The producer-scrounger game is a model of scramble kleptoparasitism - food theft with little to no aggression and simultaneous exploitation by competitors (Giraldeau and Caraco 2000, p.153) - in which individuals play one of two strategies: producers invest effort in finding resources (food, primarily, though the model can be generalized to other shareable resources), while scroungers join the discoveries of producers and share the resource. Producing and scrounging are considered to be completely *incompatible*, in that producing and scrounging cannot be played by the same player at the same time. Mathematically, the game is an n-person alternative-option scramble (Giraldeau and Caraco 2000), which is actually an extension of Hawk-Dove into an n-person game (see Chapter V).

The producer-scrounger game follows the logic of negative frequency dependent selection as outlined above: both producers and scroungers have higher fitness when they are rare, which leads to a mixed ESS solution. A graphical representation of this can be found in Figure I.3, and in fact the first producer-scrounger model (Barnard and Sibly 1981) was a graphical model that was later formalized (e.g. Parker 1984; Vickery et al. 1991; Giraldeau and Caraco 2000). There have been various mod-

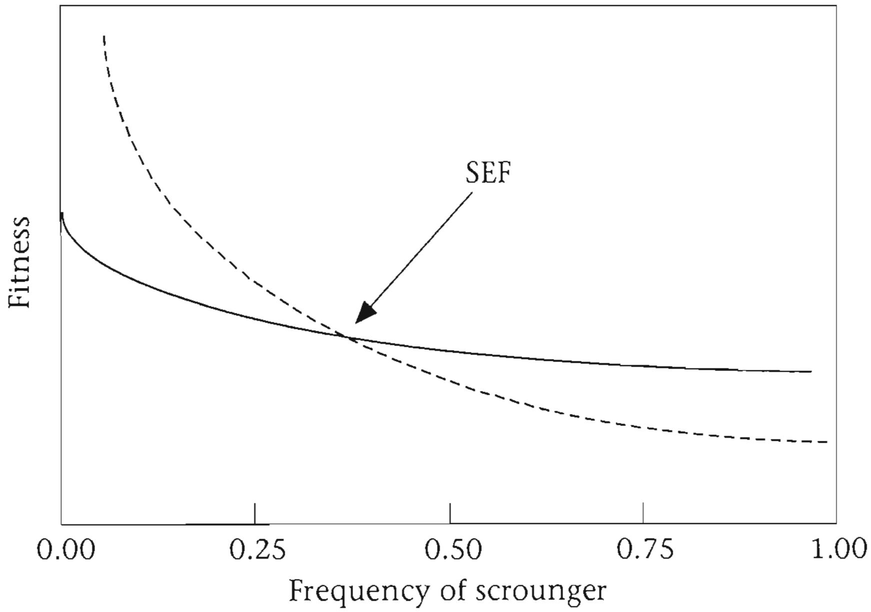

Figure 1. The payoffs of producer (solid line) and scrounger (dashed line) tactics as a function of the frequency of the scrounger tactic as expected in a producer–scrounger game. The intersection of the two payoff functions denotes what we call the stable equilibrium frequency (SEF) of the scrounger tactic. At the SEF, the payoffs to producer and scrounger are equal.

Figure I.3: Figure 1 of Mottley and Giraldeau (2000). Note the similarity to Figure I.2

ifications and extensions to the basic model, which I refer to as the Deterministic Rate-Maximizing model, or DRM, following Giraldeau and Caraco (2000). For example:

- Vickery et al. (1991) also relaxed the assumption of incompatibility by allowing *opportunists* who could play both producer and scrounger with differing efficiency.
- Ranta et al. (1996) took into account competitiveness and food-finding efficiency when extending the DRM.
- Dubois et al. (2010) used the DRM model as a basis for modelling the evolution of flexible versus fixed individuals.

- Caraco and Giraldeau (1991) presented a stochastic version of the model that focuses on the minimization of the risk of energetic shortfall; see also Giraldeau and Caraco (2000, chapter 7)

- Barta and Giraldeau (1998) introduced the 'phenotype-limited' producer-scrounger game to examine the effect of dominance.

Extending the producer-scrounger game can become complex when even basic elaborations are added, and this has led to the popularity of producer-scrounger simulation modelling (see section I.4 for a discussion on simulation methodologies). Of particular relevance to this thesis are:

- Barta et al. (1997), who used a genetic algorithm to examine the geometry of a group of producer-scrounger foragers.

- Beauchamp (2000b), who created an individual-based model to simulate learning rules in a producer-scrounger game.

- Another individual-based model is found in Beauchamp (2008), created for the purpose of simulating spatial effects on social foragers.

I.1.5 Empirical work

Do species in the wild play this game? The existence of producer-scrounger relationships has been studied in a diverse range of species; a partial list includes such species as bald eagles (Hansen 1986), shark mackerel (Auster 2008), kelp gulls (Steele and Hockey 1995), Harris sparrows (Rohwer and Ewald 1981), house sparrows (Barnard and Sibly 1981; Katsnelson et al. 2008), pigeons, (Giraldeau and Lefebvre 1986; Lefebvre and Helder 1997), carib grackles (Morand-Ferron et al. 2007), baboons (King et al. 2009), and barnacle geese (Kurvers et al. 2010), as well as nutmeg mannikins and zebra finches (Giraldeau et al. 1990). Laboratory work has focused largely on nutmeg mannikins (*Lonchura punctulata*), also known as spice finches, and zebra finches (*Taeniopygia guttata*), both of which are gregarious passerine birds found in Southeast Asia that feed on seeds typically found in discrete patches. Work on these species has confirmed some of the model's assumptions, such as the assumption of incompatibility; Coolen et al. (2001) established that nutmeg mannikins use a head-down posture when producing and a head-up posture when scrounging and showed that the proportion of head-up to head-down behaviours changed in the correct direction when the payoff to scrounging was manipulated. The interaction of producing and scrounging with other effects, such as risk sensitivity (Wu and Giraldeau 2005), prey crypticity (Barrette and Giraldeau 2006), and anti-predatory vigilance (Coolen and Giraldeau 2003; Mathot and Giraldeau 2008) has also been explored.

This thesis focuses on the theory of producer-scrounger games and so I leave an exhaustive examination of empirical work on the producer scrounger game to reviews such as Giraldeau and Caraco (2000) and Giraldeau and Dubois (2008), but empirical work of particular importance to my thesis is noted in later sections of this introduction.

I.1.6 Personality and social foraging

Animal personality is an area of behavioural ecology that has seen rapid growth in recent years (Gosling and John 1999; Koolhaas et al. 1999; Sih et al. 2004; Carere and Eens 2005; Groothuis and Carere 2005). The definition of personality is somewhat controversial (Réale et al. 2007), but a reasonable definition is 'differences between individuals in some behavioural and or physiological traits that remain consistent over time and context' (see Chapter IV). Examples of such personality traits include boldness, aggression, and proactivity (reviewed in Sih et al. 2004). Empirical evidence for the existence of animal personalities and work on their properties has accumulated quickly (Réale et al. 2007; Biro and Stamps 2008; Sih and Bell 2008), but until recently theoretical explanations of the coexistence of personality types have been scarce. New work (e.g. Wolf et al. 2007; 2008; Wolf and Weissing 2011) has placed personality on a stronger theoretical footing by suggesting methods by which frequency dependent selection could allow multiple personality types to arise and aid in their subsequent maintenance.

In the area of producer-scrounger games, this pattern of empirical and theoretical evidence has replayed itself at a smaller scale. Empirical work on barnacle geese (*Branta leucopsis*) has shown that there is a relationship between personality - boldness, in this case - and producing / scrounging tactics (Kurvers et al. 2010); bolder geese are more likely to be producers, while shy geese are more likely to be scroungers. This follows a body of work on boldness showing that bolder individuals are more likely to approach food (e.g., Beauchamp 2000a; Dyer et al. 2009; Harcourt et al. 2009; Kurvers et al. 2009; Schuett and Dall 2009). To date, though, there has been no theoretical explanation provided for a link between the producer-scrounger game and boldness, and no *a priori* reason to believe that one should exist with the producer-scrounger relationship as a causal factor. Chapter IV explores this issue by modelling social foragers playing a producer-scrounger game that vary in boldness to determine if a polymorphism of bold producers and shy scroungers arises naturally.

I.2 Information use and learning

The producer-scrounger game (section I.1) is, at its core, a game about information use. In social foraging, information may be individually-acquired (*personal information*, sometimes called *private* information) or acquired vicariously from others (*social information*; this section follows the terminology in Danchin et al. 2004). Personal information is information about an individual's world, such as the habitat and resources, that is acquired by the individual and remains private. For instance, an animal foraging alone may obtain information about a patch of food, which would be personal information. Social information, on the other hand, is information provided to others uncontrollably (inadvertent social information, or ISI) or purposely (signals). In the producer-scrounger game, inadvertent social information is provided by producers to scroungers, who use ISI to join patch discoveries.

Despite the fact that the producer-scrounger game is effectively a game with inadvertent social information as its primary driving force (Galef and Giraldeau 2001; Dall et al. 2005), when it comes to acquiring information through learning more attention has been paid to learning personal information in the game than social information. Here I will describe the use of both personal and social information in the producer-scrounger model with particular reference to areas of interest in Chapters II, III, and V.

I.2.1 Personal and social information use while learning

In the producer-scrounger game, when the decision-making process surrounding an individual's choice of tactic use has been modelled (Beauchamp 2000b), the focus has been on personal information: by playing producer and scrounger in sequence, they integrate information about the payoffs to each and make a decision about appropriate tactic use based entirely on personal information. For instance, if the producer tactic fails to payoff an individual might increase the proportion of scrounger that they use. To date, learning mechanisms discussed in the literature have centred on this idea (Beauchamp 2000b, Chapter II), but given the abundant social information available in the producer-scrounger game the absence of social learning in these models is curious, especially given empirical evidence that such learning might be occurring (Lefebvre and Helder 1997; Coolen et al. 2001).

Be that as it may, one approach to learning in behavioural ecology has focused on the evolution of 'learning rules' (literature reviewed in section I.1.3). Learning rules are mathematical expressions of the value that an individual places on each behavioural alternative available to it as a function of the payoffs it has received to that alternative; in producer-scrounger games, this translates to the valuation that foragers place on producing and scrounging from payoffs received to sampling each tactic. Work on these rules in foraging has focused on a restricted set of plausible rules, such as the Relative Payoff Sum (Harley 1981), the Perfect Memory rule (Houston and Sumida 1987), and the Linear Operator rule (Bush and Mosteller 1955, mathematical details of each rule presented in Chapter II); even restricted to these three choices, previous work on learning rules for the producer-scrounger game (Beauchamp 2000b) has not examined the relative performance of these rules against each other or their attractivity. Houston and Sumida (1987) noted that '[o]ur main concern is that we put the various rules into competition against each other. This is crucial because competition is the essence of the problem.' (p.302), and in Chapter II I have attempted to do this in a comprehensive and rigorous fashion.

While learning rules have focused on the integration of personal information to inform decision-making, other work such as the Social Learning Strategies Tournament (Rendell et al. 2010) has proposed social learning mechanisms for individual foragers and demonstrated that situations in which largely (or even entirely) ignoring personal information may be the optimal course of action. These strategies are often simple 'rules of thumb' which employ heuristic principles to solve behavioural problems such as social foraging (Simon 1957; Gigerenzer 2000; McNamara and Houston 2009). Extending the study of producer-scrounger games by employing such heuristic social learning rules is the subject of Chapter V.

I.2.2 Social information use beyond the individual

Much has been made of individual use of personal and social information (Galef and Giraldeau 2001; Danchin et al. 2004), but information use in relationships between populations or species, such as predator-prey interactions, is less well-explored. Within a group it is well known that increases in the proportion of scrounging leads to lower mean intake rates (e.g. Beauchamp and Giraldeau 1996), due to a decreased number of producers looking for food (which leads to lowered search efficiency; Coolen 2002). Coolen et al. (2007) demonstrated that the proportion of scrounging in a population can regulate that population's dynamics, but the question of whether populations can affect each other simultaneously through the manipulation of social information is largely open. Studies that have examined this issue previously have focused largely on one direction, i.e. prey response alone (e.g. Abrams 2000; Lima 2002) or predator response alone (Murdoch 1973; Readshaw 1973; Ryer and Olla 1995; Cosner et al. 1999; Bonmarco et al. 2007). In the study in Chapter III, I explore this question in greater detail by asking whether prey can manipulate the use of social information in predators playing a producer-scrounger game; in particular, can prey evolve to manipulate the use of scrounging in predators, lowering predator efficiency and increasing prey survival?

I.2.3 Empirical work on learning in producer-scrounger games

I am not aware of any studies which have directly tested the predictions of learning rules in producer-scrounger games (though some tests have been done in other foraging scenarios, e.g.: Regelmann 1984; Wildhaber and Crowder 1991; Amano et al. 2006), though observations have been made which indicate that learning is indeed taking place. In one study of particular interest, Mottley and Giraldeau (2000) tested nutmeg mannikins using an apparatus that allowed them to control the payoffs to the producer and scrounger tactics and discovered that the birds were able to adjust their behaviour over time to reach the stable equilibrium frequency (SEF); this study confirmed the equality of payoffs to the two tactics at equilibrium and demonstrated that nutmeg mannikins were able to learn the equilibrium and change their behaviour when local conditions changed. Katsnelson et al. (2008) later found that house sparrows could be biased in their tactic use by early manipulation of their experienced payoffs, and this relationship was explored in nutmeg mannikins by Morand-Ferron and Giraldeau (2010), who found that nutmeg mannikins who had been exposed to high payoffs to scrounging used more scrounger behaviour in subsequent trials where scrounging had lower payoffs compared to individuals who had been exposed to low scrounging payoffs to begin with. The form of the mechanism underlying this learning remains open, however, and is the subject of Chapters II and V.

I.3 Social foragers in space

In what is otherwise an excellent volume, a recent textbook on animal foraging (Stephens et al. 2007) features a surprising omission: not a single chapter deals substantively with spatial processes in foraging, and the entire book contains only a few passing mentions of the topic at all. This is not an isolated problem; indeed, the standard reference text on social foraging (Giraldeau and Caraco 2000) does not have a single mention of the concept in its index. This is an odd oversight, given that foraging is one of the most obviously spatial concepts in behavioural ecology, yet the majority of social foraging models have focused exclusively on time and ignored space (Lima and Zollner 1996; Valcu and Kempanaers 2010). Even models such as the ideal free distribution (Harper 1982), which are inherently spatial, are presented without an explicit description of the underlying spatial process for resources or consumers (e.g. Sutherland 1983; Cressman et al. 2004).

Producer-scrounger games are subject to this problem as well, as evidenced by the deterministic rate-maximizing model discussed in Giraldeau and Caraco (2000). The model contains assumptions which deliberately abstract spatial issues out of the game, but this creates its own problems. As an example, the model assumes that patch handling time is negligible and also that patch discoveries happen with a rate low enough that the chance of simultaneous discovery by producers is effectively zero; this eliminates problems related to the distribution of scroungers between patches, but clearly does not match observations in empirical work. The consequence of that assumption is another assumption in turn: every scrounger joins the food discovery of every producer, which presents no problems to a non-spatial model but is an issue when spatial scale is introduced. The distortions introduced by these assumptions are less disruptive if group sizes and spatial extents are small, as they often are in laboratory observations conducted in small aviaries with flocks numbering no more than six or eight birds (a common enough occurrence: Giraldeau et al. 1990; 1994; Mottley and Giraldeau 2000; Gauvin and Giraldeau 2004; Wu and Giraldeau 2005; Barrette and Giraldeau 2006, among others), but satisfying these same assumptions in any real environment would likely require birds of unrealistic speed and cognitive ability. A common study species for laboratory observations is the zebra finch, but as Zann (1996) notes, foraging flocks in wild zebra finch populations can number in the hundreds. Further, aviary conditions in which individuals forage on square grids with regularly spaced patches laid out in a grid format ignore the spatial heterogeneity that animals foraging in real landscapes face; this problem is replicated in the entire body of simulation work that has been done on the problem (including the work discussed below; Chapter VI explores the issues in detail). Mapping predictions from classical producer-scrounger models onto such populations of animals foraging in real landscapes will be a difficult challenge without spatially-explicit models.

To date, few attempts have been made to address the issue in the study of producer-scrounger games or social foraging in general. Ruxton (1995) was among the first to make a coherent call to address the problem, and presented a spatially-explicit simulation model for group foragers. Although Ruxton noted that spatial processes had significant effects on the time taken by foragers to discover patches and join others who have done so ("[i]t seems likely that sharing patches discovered by other individuals may not always benefit a forager because of the cost of travelling to the discovered patch", p. 284), the paper seems to have been largely ignored.

A more well-known model was published by Barta et al. (1997), wherein the authors modelled the geometry of a producer-scrounger flock and predicted that producers would be found near the outside of the flock and scroungers would concentrate near the centre. Curiously, though, despite focusing on flock geometry, the paper adopts the same 'teleporting' scroungers as in the classical models, which dilutes the spatial explicitness of their representation. Regardless, the model has played an important part in the producer-scrounger literature , and its predictions were qualitatively verified by a follow-up empirical study (Flynn and Giraldeau 2001).

The only other spatially explicit model to be published in recent years is an effort by Beauchamp (2008), who created an individual-based model to study the problem. Unfortunately, in work not presented in this thesis (MS in prep.) I discovered that the results of this study are not replicable.

The most likely reason for this systematic omission is the difficulty in creating tractable models which contain such explicit spatial mechanisms. Models with analytical solutions are largely out of reach to current techniques, but a new generation of simulation methodology has grown up to help alleviate this problem (see section I.4), and the chapters of my thesis reflect these new techniques.

I.4 Modelling methodology

Contributing to the collected work on producer-scrounger models has required using simulation and computational methods of some complexity; these methods are increasing in popularity in biology and behavioural ecology in general, but their use still benefits from introduction and explanation. In this section, I provide an overview and brief description of the methods used in the thesis: individual-based models, genetic algorithms, and cellular automata.

I.4.1 Individual-based models

Forming the core of each of Chapters II,III, and IV is an individual-based model (IBM; also known as an agent-based model or ABM). An individual-based model is a computational model of the actions and interactions of individuals, usually implemented by specifying rules of behaviour for individuals and simulating their interaction to see the effects on those individuals and the system as a whole (Grimm and Railsback 2005). Individual-based models have many positive attributes, including the ability to simulate complex systems beyond the reach of analytical models and the chance to study emergent properties of those systems (Judson 2003; DeAngelis and Mooij 2005); negatives include difficulties in interpretation (Seth 2007) and the sometimes massive computational requirements for modelling systems of interest.

In foraging theory, individual-based models allow us to easily simulate social foraging in a spatially explicit world (e.g. Ruxton 1995; Beauchamp and Giraldeau 1996; Beauchamp 2000b, Chapters II, III, IV), a task which has yet escaped capture by a tractable analytical model.

I.4.2 Genetic algorithms

Genetic algorithms are simulations which mimic the action of natural selection to solve optimization problems (Mitchell 1998). Populations of individual candidate solutions ('chromosomes') are generated randomly and their ability to solve an optimization problem is assessed; chromosomes which prove to be better solutions to the problem are assigned higher 'fitness' values. After fitness evaluation, the candidate solutions / chromosomes undergo selection and reproduction to form a new population, modified by the genetic operators of mutation and / or recombination. As the simulation progresses through generations, solutions with higher fitness reproduce in greater proportions and the population converges on fitness peaks in the adaptive landscape; unlike simpler hill-climbing algorithms, genetic algorithms have the ability to avoid local optima by 'jumping' over fitness valleys using mutation and recombination (Mitchell 1998).

The use of genetic algorithms in behavioural biology was called for over twenty years ago (Sumida et al. 1990), but the answer to that call was slow in coming. In recent years, however, genetic algorithms have seen use in problems such as foraging (Barta et al. 1997, Chapters II and IV), the study of cooperation (Crowley et al. 1996; Crowley 1996), vigilance (Ruxton and Beauchamp 2008), mate choice (Collins et al. 2006), and signalling (Hamblin and Hurd 2007; 2009; Szalai and Számadó 2009), and urgings to adopt genetic algorithm approaches for complex problems (especially those involving game theory) have appeared (Hamblin and Hurd 2007; Ruxton and Beauchamp 2008).

It should be noted that Chapter III features an unusual use of genetic algorithms in biology (and, indeed, elsewhere), as it uses two co-evolving genetic algorithms to model the coevolution of the predator-prey problem of interest. I am not aware of another example of this in the literature of behavioural biology, though the technique is used in computer science and bioinformatics circles (e.g. Lohn et al. 2002).

I.4.3 Cellular automata

Cellular automata are discrete-time models in which individuals are embedded on a grid in one of a finite set of states and interact with their immediate neighbours in a way that is defined by their *update rule*; update rules define the state that individuals will be in after their current time step is completed (Wolfram 1984). Cellular automata are usually (but not always: Moyano and Sánchez 2009) deterministic, meaning that given the same input it is possible to replicate the results of that input at will, even if the results cannot be predicted ahead of time.

By far the most famous example of a cellular automata is John Conway's Game of Life (described in Gardner 1970), which has simple genetic rules: the game is played on an infinite two-dimensional grid of cells, each of which is either alive or dead in any time step. The update rules for the grid are: a cell with two or three live neighbours survives to the next time step, a cell with two or less live neighbours dies (starvation) as does a cell with four or more live neighbours (overcrowding), and a dead cell with three live neighbours becomes alive in the next time step (reproduction). The rules are depicted in Figure I.4, along with two beginning patterns that do not immediately fade.

From simple rules, the Game of Life can give rise to patterns of impressive complexity, and it has been a source of much interest and research; recently, a self-replicating pattern that constructs a new copy of itself with a generation time of 34 million time steps was discovered (Groucher 2010).

Cellular automata have also been combined with evolutionary game theory to explore the dynamics of simple frequency dependent games. Nowak and May (1992) constructed and analyzed a cellular automata to play the Prisoner's Dilemma game (a well-studied game that models the evolution of cooperation; Nowak 2006). In the basic one-shot Prisoner's Dilemma game cooperation cannot easily evolve, but when played as a cellular automata the resulting dynamics showed chaotic complexity that led to indefinite co-existence of both cooperation and defection. The power of this approach inspired the model of social learning in the producer-scrounger game that is presented in Chapter V.

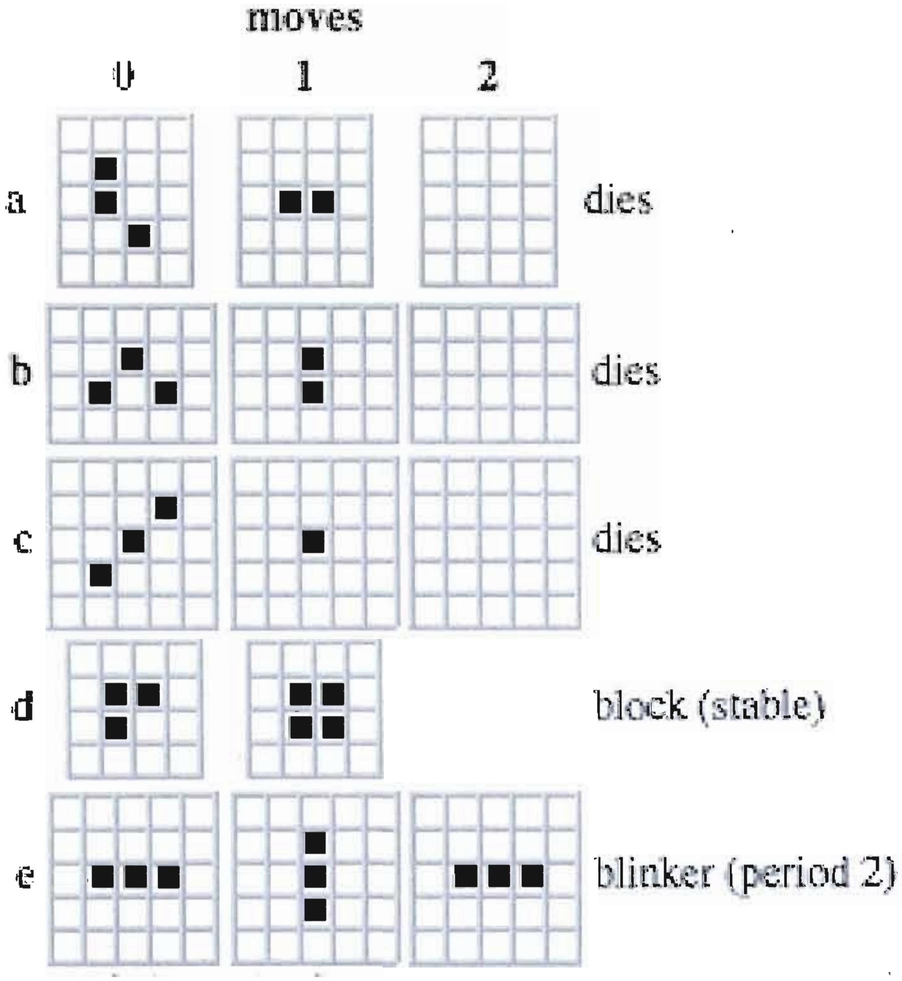

Figure I.4: Figure 1 of Gardner (1970).

I.5 Thesis overview

The articles in this thesis form my attempt to contribute to the study of social foraging in general and producer-scrounger games in particular. Three broad themes will be evident in the studies presented in the following chapters. The first is the addition of needed complexity to the body of producer-scrounger theory: learning rules, coevolutionary pressures, personality, and social learning. The second broad theme is information use, both personal (learning rules; Chapter II) and social (coevolution of information use and social learning; Chapters III and V); even Chapter IV on personality and producer-scrounger games contains items of interest for information use in its results. Finally, an important issue that acts as a substrate for this thesis is the effect of space on the producer-scrounger models. Every model presented in this thesis is spatially-explicit, and this spatial aspect has ramifications for the results of each chapter that will be dealt with not only in the individual chapters but in the conclusion of the thesis as well.

In Chapter II, I attempt to clarify previous work on learning rules for social foraging (Beauchamp 2000b) by testing the attractiveness and stability of previously proposed learning rules in an individual-based model of producing and scrounging. By testing the rules in competition with each other and using a genetic algorithm to select the rule with the best performance, I was able to provide evidence that Harley (1981)'s initial claims about an ES learning rule - overreaching as they may have been at the time - were true, and that the rule took the form he predicted; I was also able to generate new predictions for empirical work based on patterns observed in the results on the evolution of the rule parameters.

In Chapter III, I show how the co-evolution of predator-prey population dynamics can influence information use in predators as a function of prey trait evolution (clumping); this response to prey trait evolution led to changes in predator search efficiency and in turn changes in prey survival rates. The model I constructed for this effort used a set of two co-evolving genetic algorithms coupled to an individual-based model in order to allow prey and predators to evolve against each other.

In Chapter IV, I use a genetic algorithm on top of an individual-based model to explore the relationship of the animal personality trait boldness to the producing and scrounging tactics in order to determine if the bold producer / shy scrounger dimorphism seen in empirical work (Kurvers et al. 2010) would occur. This model allowed us to explore the relationship between boldness and social foraging thoroughly and provided evidence regarding the probable form of the link between the two variables.

Following this, in Chapter V, I present a novel producer-scrounger model in the form of a cellular automata that uses a social learning 'rule of thumb' as a mechanism for decision-making about tactic choice. The model also has interesting spatial characteristics and population dynamics that have implications for the study of producer-scrounger systems in future empirical and theoretical work.

Finally, Chapter VI presents a model that I developed to explore the effect of landscape geometry (the way that space is represented, which in extant work has been as a square grid) on producing and scrounging. The model demonstrates the impact of spatial heterogeneity on ESS outcomes, flock geometry, and feeding rates as part of a broader argument about the generalization of producer-scrounger models to real foraging situations.

Chapter VII provides a synthesis of the thesis material and a discussion of key findings and and how they related to the themes of the thesis. I identify the contributions to the study of producer-scrounger games and social foraging that my work has produced, and discuss directions for future research.

I.6 Bibliography

Abrams, P. A. (2000). The impact of habitat selection on the spatial heterogeneity of resources in varying environments. *Ecology*, 81:2902–2913.

Amano, T., Ushiyama, K., Moriguchi, S., Fujita, G., and Higuchi, H. (2006). Decision-making in group foragers with incomplete information: Test of individual-based model in geese. *Ecological Monographs*, 76(4):601–616.

Auster, P. (2008). Variation in search and predatory attack strategies of shark mackerel *Grammatorcynus bicarnatus*. *Journal of the Marine Biological Association of the United Kingdom*, 88(4):847–849.

Barnard, C. J. and Sibly, R. M. (1981). Producers and scroungers: A general model and its application to captive flocks of house sparrows. *Animal Behaviour*, 29:543–550.

Barrette, M. and Giraldeau, L.-A. (2006). Prey crypticity reduces the proportion of group members searching for food. *Animal Behaviour*, 71:1183–1189.

Barta, Z., Flynn, R., and Giraldeau, L.-A. (1997). Geometry for a selfish foraging group: a genetic algorithm approach. *Proceedings of the Royal Society of London. Series B, Biological Sciences*, 264:1233–1238.

Barta, Z. and Giraldeau, L.-A. (1998). The effect of dominance hierarchy on the use of alternative foraging tactics: a phenotype-limited producing-scrounging game. *Behavioural Ecology and Sociobiology*, 42:217–223.

Beauchamp, G. (2000a). Individual differences in activity and exploration influence leadership in pairs of foraging zebra finches. *Behaviour*, 137:301–314.

Beauchamp, G. (2000b). Learning rules for social foragers: Implications for the producer-scrounger game and ideal free distribution theory. *Journal of Theoretical Biology*, 207:21–35.

Beauchamp, G. (2008). A spatial model of producing and scrounging. *Animal Behaviour*, 76:1935–1942.

Beauchamp, G. and Giraldeau, L.-A. (1996). Group foraging revisited: Information sharing or producer-scrounger game? *The American Naturalist*, 148(4):738–743.

Biro, P. A. and Stamps, J. A. (2008). Are animal personality traits linked to life-history productivity? *Trends in Ecology & Evolution*, 23(7):361–368.

Bonmarco, R., Firle, S. O., and Ekbom, B. (2007). Outbreak suppression by predators depends on spatial distribution of prey. *Ecological Modelling*, 201(2):163–170.

Bush, R. and Mosteller, F. (1955). *Stochastic models for learning*. New York. Wiley.

Caraco, T. and Giraldeau, L.-A. (1991). Social foraging: Producing and scrounging in a stochastic environment. *Journal of Theoretical Biology*, 153:559–583.

Carere, C. and Eens, M. (2005). Unravelling animal personalities: how and why individuals consistently differ. *Behaviour*, 142(9):1149–1157.

Collins, E. J., McNamara, J. M., and Ramsey, D. D. (2006). Learning rules for optimal selection in a varying environment: mate choice revised. *Behavioral Ecology*, 17:799–809.

Coolen, I. (2002). Increasing foraging group size increases scrounger use and reduces searching efficiency in nutmeg mannikins (*Loncura punctulata*). *Behavioural Ecology and Sociobiology*, 52:232–238.

Coolen, I. and Giraldeau, L.-A. (2003). Incompatibility between antipredatory vigilance and scrounger tactic in nutmeg mannikins, *Lonchura punctulata*. *Animal Behaviour*, 66:657–664.

Coolen, I., Giraldeau, L.-A., and Lavoie, M. (2001). Head position as an indicator of producer and scrounger tactics in a ground-feeding bird. *Animal Behaviour*, 61:895–903.

Coolen, I., Giraldeau, L.-A., and Vickery, W. L. (2007). Scrounging behavior regulates population dynamics. *Oikos*, 116:533–539.

Cosner, C., Deangelis, D. L., Ault, J. S., and Olson, D. B. (1999). Effects of spatial grouping on the functional responses of predators. *Theoretical Population Biology*, 56:65–75.

Cressman, R., Křivan, V., and Garay, J. (2004). Ideal free distributions, evolutionary games, and population dynamics in multiple-species environments. *The American Naturalist*, 164(4):473–489.

Crowley, P. H. (1996). Evolving cooperation: strategies as hierarchies of rules. *Biosystems*, 37(1-2):67–80.

Crowley, P. H., Provencher, L., Sloane, S., Dugatkin, L. A., Spohn, B., Rogers, L., and Alfieri, M. (1996). Evolving cooperation: the role of individual recognition. *Biosystems*, 37(1-2):49–66.

Dall, S. R. X., Giraldeau, L.-A., Olsson, O., McNamara, J. M., and Stephens, D. W. (2005). Information and its use by animals in evolutionary ecology. *TRENDS in Ecology and Evolution*, 20(4):187–193.

Danchin, É., Giraldeau, L.-A., Valone, T. J., and Wagner, R. H. (2004). Public information: from nosy neighbors to cultural evolution. *Science*, 305:487–491.

Dawkins, R. (1976). *The selfish gene.* Oxford University Press.

DeAngelis, D. L. and Mooij, W. M. (2005). Individual-based modeling of ecological and evolutionary processes. *Annual Review of Ecology, Evolution, and Systematics*, 36(1):147–168.

Dubois, F., Morand-Ferron, J., and Giraldeau, L.-A. (2010). Learning in a game context: strategy choice by some keeps learning from evolving in others. *Proceedings of the Royal Society of London. Series B, Biological Sciences*, 277:3609–3616.

Dyer, J. R. G., Croft, D. P., Morrell, L. J., and Krause, J. (2009). Shoal composition determines foraging success in the guppy. *Behavioral Ecology*, 20(1):165–171.

Flynn, R. and Giraldeau, L.-A. (2001). Producer-scrounger games in a spatially explicit world: Tactic use influences flock geometry of spice finches. *Ethology*, 107:249–257.

Galef, B. G. and Giraldeau, L.-A. (2001). Social influences on foraging in vertebrates: causal mechanisms and adaptive functions. *Animal Behaviour*, 61:3–15.

Gardner, M. (1970). Mathematical games: The fantastic combinations of John Conway's new solitaire game "Life". *Scientific American*, 223:120–123.

Gauvin, S. and Giraldeau, L.-A. (2004). Nutmeg mannikins (*lonchura punctulata*) reduce their feeding rates in response to simulated competition. *Oecologia*, 139:150–156.

Gigerenzer, G. (2000). *Adaptive thinking: Rationality in the real world.* Oxford University Press, New York, NY.

Giraldeau, L.-A. and Caraco, T. (2000). *Social Foraging Theory.* Monographs in Behavior and Ecology. Princeton University Press, New Jersey.

Giraldeau, L.-A. and Dubois, F. (2008). Social foraging and the study of exploitative behaviour. In Brockmann, H. J., Snowdon, C. T., Roger, T. J., Naquib, M., and Wynne-Edwards, K. E., editors, *Advances in the study of behavior*, volume 38, pages 59–104. Elsevier.

Giraldeau, L.-A., Hogan, J. A., and Clinchy, M. J. (1990). The payoffs to producing and scrounging: What happens when patches are divisible? *Ethology*, 85:132–146.

Giraldeau, L.-A. and Lefebvre, L. (1986). Exchangeable producer and scrounger roles in a captive flock of feral pigeons: a case for the skill pool effect. *Animal Behavior*, 34(797-803).

Giraldeau, L.-A. and Livoreil, B. (1998). Game theory and social foraging. In Dugatkin, L. A. and Reeve, H. K., editors, *Game theory and animal behaviour.*, pages 16–37. Oxford University Press, New York.

Giraldeau, L.-A., Soos, C., and Beauchamp, G. (1994). A test of the producer-scrounger foraging game in captive flocks of spice finches, *Lonchura punctulata. Behavioural Ecology and Sociobiology*, 34(251-256).

Gosling, S. D. and John, O. P. (1999). Personality dimensions in nonhuman animals: a cross-species review. *Current Directions in Psychological Science*, 8(3):69–75.

Grimm, V. and Railsback, S. F. (2005). *Individual-based Modeling and Ecology.* Princeton University Press, Princeton, NJ.

Groothuis, T. G. G. and Carere, C. (2005). Avian personalities: characterization and epigenesis. *Neuroscience and Biobehavioral Reviews*, 29(1):137–150.

Groucher, A. P. (2010). Oblique Life spaceship created. `http://pentadecathlon.com/lifeNews/2010/05/oblique_life_spaceship_created.html`.

Hamblin, S. and Hurd, P. L. (2007). Evolution's strategies: Genetic algorithms and game theory models. *Animal Behaviour*, 74(4):1005–1018.

Hamblin, S. and Hurd, P. L. (2009). When will evolution lead to deceptive signaling in the sir philip sidney game? *Theoretical Population Biology*, 75(176-182).

Hammerstein, P. (1998). What is evolutionary game theory? In Dugatkin, L. A. and Reeve, H. K., editors, *Game theory and animal behaviour.*, pages 3–15. Oxford University Press, New York.

Hansen, A. J. (1986). Fighting behavior in bald eages: A test of game theory. *Ecology*, 67(3):787–797.

Harcourt, J. L., Ang, T. Z., Sweetman, G., Johnstone, R. A., and Manica, A. (2009). Social feedback and the emergence of leaders and followers. *Current Biology*, 19(3):248–252.

Harley, C. B. (1981). Learning the evolutionarily stable strategy. *Journal of Theoretical Biology*, 89:611–633.

Harley, C. B. (1983). When do animals learn the evolutionarily stable strategy? *Journal of Theoretical Biology*, 105:179–181.

Harley, C. B. (1987). Learning rules, optimal behaviour, and evolutionary stability. *Journal of Theoretical Biology*, 127:377–379.

Harper, D. G. C. (1982). Competitive foraging in mallards: 'ideal free' ducks. *Animal Behaviour*, 30:575–584.

Houston, A. I. (1983). Comments on "learning the evolutionarily stable strategy". *Journal of Theoretical Biology*, 105:175–178.

Houston, A. I. and Sumida, B. H. (1987). Learning rules, matching, and frequency dependence. *Journal of Theoretical Biology*, 126:289–308.

Judson, O. P. (2003). The rise of the individual-based model in ecology. *Trends in Ecology & Evolution*, 9(1):9–14.

Katsnelson, E., Motro, U., Feldman, M. W., and Lotem, A. (2008). Early experience affects producer-scrounger foraging tendences in the house sparrow. *Animal Behaviour*, 75:1465–1472.

King, A. J., Isaac, N. J. B., and Cowlishaw, G. (2009). Ecological, social and reproductive factors shape producer-scrounger dynamics in baboons. *Behavioral Ecology*.

Koolhaas, J. M., Korte, S. M., de Boer, S. F., Vegt, B. J. V. D., Reenen, C. G. V., Hopster, H., Jong, I. C. D., Ruis, M. A. W., and Blokhuis, H. J. (1999). Coping styles in animals: current status in behavior and stress-physiology. *Neuroscience and Biobehavioral Reviews*, 23:925–935.

Kurvers, R. H., Eijkelenkamp, B., van Oers, K., van Lith, B., van Wieren, S. E., Ydenberg, R. C., and Prins, H. H. (2009). Personality differences explain leadership in barnacle geese. *Animal Behaviour*, 78(2):447–453.

Kurvers, R. H., Prins, H. H., van Wieren, S. E., van Oers, K., Nolet, B. A., and Ydenberg, R. C. (2010). The effect of personality on social foraging: shy barnacle geese scrounge more. *Proceedings of the Royal Society of London. Series B, Biological Sciences*, 277(1681):601–608.

Lefebvre, L. and Helder, R. (1997). Scrounger numbers and the inhibition of social learning in pigeons. *Behavioural Processes*, 40:201–207.

Lima, S. L. (2002). Putting predators back into behavioral predator-prey interactions. *TRENDS in Ecology and Evolution*, 17(2):70–75.

Lima, S. L. and Zollner, P. A. (1996). Towards a behavioral ecology of ecological landscapes. *Trends in Ecology & Evolution*, 11(3):131–135.

Lohn, J., Kraus, W., and Haith, G. (2002). Comparing a coevolutionary genetic algorithm for multiobjective optimization. *Proceedings of the 2002 IEEE Congress on Evolutionary Computation.*, pages 1157–1162.

Mathot, K. J. and Giraldeau, L.-A. (2008). Increasing vulnerability to predation increases preference for the scrounger foraging tactic. *Behavioral Ecology*, 19(1):131–138.

Maynard Smith, J. (1972). Game theory and the evolution of fighting. In Maynard Smith, J., editor, *On Evolution*. Edinburgh University Press.

Maynard Smith, J. (1982). *Evolution and the Theory of Games*. Cambridge University Press, New York, NY.

Maynard Smith, J. and Price, G. R. (1973). The logic of animal conflict. *Nature*, 246(1):15–18.

McNamara, J. M. and Houston, A. I. (2009). Integrating function and mechanism. *Trends in Ecology & Evolution*, 24(12):670–675.

Mitchell, M. (1998). *An introduction to genetic algorithms*. MIT Press, Cambridge, Massachusetts, 1st paperback edition edition.

Morand-Ferron, J. and Giraldeau, L.-A. (2010). Learning behaviorally stable solutions to producer-scrounger games. *Behavioral Ecology*, 21(2):343–348.

Morand-Ferron, J., Giraldeau, L.-A., and Lefebvre, L. (2007). Wild carib grackles play a producer-scrounger game. *Behavioral Ecology*, 18(5):916–921.

Mottley, K. and Giraldeau, L.-A. (2000). Experimental evidence that group foragers can converge on predicted producer-scrounger equilibria. *Animal Behaviour*, 60:341–350.

Moyano, L. G. and Sánchez, A. (2009). Evolving learning rules and emergence of cooperation in spatial prisoner's dilemma. *Journal of Theoretical Biology*, 259:84–95.

Murdoch, M. W. (1973). Functional response of predators. *Journal of Applied Ecology*, 10:335–342.

Nowak, M. A. (2006). *Evolutionary Dynamics: Exploring the Equations of Life*. Harvard University Press, Cambridge, Massachusetts.

Nowak, M. A. and May, R. M. (1992). Evolutionary games and spatial chaos [letter to the editor]. *Nature*, 359(4):826–829.

Parker, G. A. (1984). The producer/scrounger model and its relevance to sexuality. In Barnard, C. J., editor, *Producers and scroungers: Strategies of exploitation and parasitism.*, pages 127–153. Chapman & Hall, New York.

Ranta, E., Peuhkuri, N., Laurila, A., Rita, H., and Metacalfe, N. B. (1996). Producers, scroungers, and foraging group structure. *Animal Behaviour*, 51:171–175.

Readshaw, J. L. (1973). Numerical response of predators to prey density. *Journal of Applied Ecology*, 10:342–351.

Réale, D., Reader, S. M., Sol, D., McDougall, P. T., and Dingemanse, N. J. (2007). Integrating animal temperament within ecology and evolution. *Biological Reviews*, 82(2):291–318.

Regelmann, K. (1984). Competitive resource sharing: A simulation model. *Animal Behaviour*, 32:226–232.

Rendell, L., Boyd, R., Cownden, D., Enquist, M., Eriksson, K., Feldman, M. W., Fogarty, L., Ghirlanda, S., Lillicrap, T., and Laland, K. N. (2010). Why copy others? insights from the social learning strategies tournament. *Science*, 328:208–213.

Rice, S. H. (2004). *Evolutionary theory: mathematical and conceptual foundations.* Sinauer Associates, Inc., Massachusetts.

Rohwer, S. and Ewald, P. W. (1981). The cost of dominance and advantage of subordination in a badge signaling system. *Evolution*, 35(3):441–454.

Ruxton, G. D. (1995). Foraging in flocks: non-spatial models may neglect important costs. *Ecological Modelling*, 82:277–285.

Ruxton, G. D. and Beauchamp, G. (2008). The application of genetic algorithms in behavioural ecology, illustrated with a model of anti-predator vigilance. *Journal of Theoretical Biology*, 250:435–448.

Ryer, C. H. and Olla, B. L. (1995). Influences of food distribution on fish foraging behaviour. *Animal Behaviour*, 49:411–418.

Schuett, W. and Dall, S. R. X. (2009). Sex differences, social context and personality in zebra finches, *Taeniopygia guttata*. *Animal Behaviour*, 77:1041–1050.

Seth, A. K. (2007). The ecology of action selection: Insights from artificial life. *Philosophical Transactions of the Royal Society, Biological Sciences*, 362:1545–1558.

Sih, A. and Bell, A. (2008). Insights for behavioral ecology from behavioral syndromes. *Advances in the Study of Behaviour*, 38:227–281.

Sih, A., Bell, A., and Johnson, J. C. (2004). Behavioural syndromes: An ecological and evolutionary overview. *TRENDS in Ecology and Evolution*, 19(7):371–377.

Simon, H. A. (1957). *Models of man: Social and rational.* John Wiley and Sons, Inc., New York.

Steele, W. K. and Hockey, P. A. R. (1995). Factors influencing rate and success of intraspecific kleptoparasitism among Kelp gull (*Larus dominicanus*). *The Auk*, 112(4):847–859.

Stephens, D. W., Brown, J. S., and Ydenberg, R. C., editors (2007). *Foraging: behavior and ecology.* University of Chicago Press, Chicago.

Stephens, D. W. and Krebs, J. R. (1986). *Foraging theory.* Monographs in Behavior and Ecology. Princeton University Press, New Jersey.

Sumida, B. H., Houston, A. I., McNamara, J. M., and Hamilton, W. D. (1990). Genetic algorithms and evolution. *Journal of Theoretical Biology*, 147:59–84.

Sutherland, W. J. (1983). Aggregation and the 'ideal free' distribution. *The Journal of Animal Ecology*, 52(3):821–828.

Szalai, F. and Számadó, S. (2009). Honest and cheating strategies in a simple model of aggressive communication. *Animal Behaviour*, 78:949–959.

Tracy, N. D. and Seaman Jr., J. W. (1995). Properties of evolutionarily stable learning rules. *Journal of Theoretical Biology*, 177:193–198.

Valcu, M. and Kempanaers, B. (2010). Spatial autocorrelation: an overlooked concept in behavioral ecology. *Behavioral Ecology*, 21(5):902–905.

Vickery, W. L., Giraldeau, L.-A., Templeton, J. J., Kramer, D. L., and Chapman, C. A. (1991). Producers, scroungers, and group foraging. *The American Naturalist*, 137(6):847–863.

Wildhaber, M. L. and Crowder, L. B. (1991). Mechanisms of patch choice by bluegills (*Lepomis macrochirus*): Foraging in a variable environment. *Copeia*, 1991(2):445–460.

Wolf, M., van Doorn, G. S., Leimar, O., and Weissing, F. J. (2007). Life-history trade-offs favour the evolution of animal personalities. *Nature*, 447(581-585).

Wolf, M., van Doorn, G. S., and Weissing, F. J. (2008). Evolutionary emergence of responsive and unresponsive personalities. *Proceedings of the National Academy of Sciences*, 105(41):15825–15830.

Wolf, M. and Weissing, F. J. (2011). An explanatory framework for adaptive personality differences. *Philosophical Transactions of the Royal Society, Biological Sciences*, 365:3959–3968.

Wolfram, S. (1984). Cellular automata as models of complexity. *Nature*, 311(4):419–424.

Wu, G.-M. and Giraldeau, L.-A. (2005). Risky decisions: a test of risk sensitivity in socially foraging flocks of lonchura punctulata. *Behavioural Ecology*, 16(1):8–14.

Zann, R. A. (1996). *The zebra finch: A synthesis of field and laboratory studies*. Oxford Ornithology Series. Oxford University Press, Oxford.

CHAPTER II

LEARNING RULES FOR SOCIAL FORAGING

Preamble

This chapter is an article published in the journal *Animal Behaviour* (Vol. 78, pp. 1343-1350). Steven Hamblin formulated the research question, developed the model and conducted the simulations, analyzed the results and wrote the first draft of the paper. Luc-Alain Giraldeau provided feedback and guidance throughout the project, and helped revise the paper for publication.

Finding the evolutionarily stable learning rule for frequency-dependent foraging.

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II.1 Abstract

The cognitive mechanisms by which an organism comes to employ an optimal response to a situation are of great interest in behavioural ecology, but the basis and form of these mechanisms have been little studied. One approach employs learning rules, mathematical expressions that calculate the value of the behavioural alternatives in an organism's repertoire based on past and present rewards to those alternatives. Previous work on these learning rules has examined the performance of rules to determine whether they can achieve evolutionarily stable optimums. However, not only has this work tested rules in isolation, but the parameter values chosen to test them have been few and chosen arbitrarily. Moreover, the environments in which the rules have been evaluated are unchanging, a condition that does not favour learning. In this study we extend simulation work on three learning rules (Relative Payoff Sum, Linear Operator, and Perfect Memory. We use a genetic algorithm to both estimate the optimal parameter values for each rule and place the rules in competition with each other in a foraging game with a changing environment. Our results confirm earlier findings that the relative payoff sum is an ES learning rule. However, the results go much further because they show that the form of the learning rule that qualifies as evolutionarily stable combines near inextinguishable producing with highly responsive scrounging. The relative payoff sum may provide a single rule that can account for the way an animal's ecology can come to affect its specific set of learning sensitivities.

II.2 Introduction

In the course of their daily activities many animals are faced with choices. These may concern habitat selection, the exploitation of food patches, selecting prey to attack or mates to court or even opponents with whom to compete. The expected fitness return from such decisions depends on the information that is available to the animal and how it is used to decide on a course of action. When the value of alternatives is uncertain and changes over time, animals collect information or sample before deciding on a course of action. Selection is expected to have favoured individuals capable of acquiring information and acting appropriately (Stephens 1991). Models of optimal sampling under mostly non-social circumstances have been proposed and supported experimentally (Shettleworth et al. 1988).

In social situations sampling can become more difficult because the values of alternative courses of action not only depend on how the environment changes over time but also on the decisions of others (Giraldeau and Caraco 2000). In such cases sampling is best analyzed as an evolutionary game (Maynard Smith 1982). For example, an animal foraging for two prey types may face uncertainty concerning the abundance of either prey type. But if it forages in the company of others, it must also contend with the changing abundances that will be induced by the prey selection decisions of its competitors. Determining which prey selection policy provides the greater payoff will require some sampling and adjustment of decision as conditions change.

The rule that governs an animal's sampling and its influence on decision in the context of games has been labelled a "learning rule" (Harley 1981). Learning rules are mathematical descriptions of how animals assign values to behavioural alternatives based on current and past information about their payoffs obtained by sampling. Maynard Smith (1982) and Harley (1981) argued that natural selection would favour learning rules that led the group most quickly to the expected evolutionarily stable strategy: the ESS (Maynard Smith 1982). They defined an evolutionarily stable (ES) learning rule (Harley 1981) as a rule which, once fixed in a group, could not be invaded by any "mutant" rule. An ES learning rule, if one exists, would prove an extremely powerful tool for predicting the strategic use of alternative behaviour by animals engaged in games such as cooperation, fighting, habitat choice and resource exploitation (Dugatkin and Reeve 1997).

Maynard Smith (1982) and Harley (1981) proposed that one learning rule, the Relative Payoff Sum (RPS), was a strong contender for the title of an ES learning rule. Not too surprisingly, therefore, a considerable amount of research has been focused on testing the evolutionary stability of the RPS and other rules; some theoretical (Harley 1983; Houston 1983; Hines and Bishop 1983; Harley 1987; Houston and Sumida 1987; Tracy and Seaman Jr. 1995), some empirical (e.g. Milinski 1984; Kacelnik and Krebs 1985; Amano et al. 2006), and some using computer simulation (e.g. Regelmann 1984; Beauchamp 2000; Beauchamp and Fernández-Juricic 2004; Beauchamp 2004; Beggs 2005; Amano et al. 2006; Spataro and Bernstein 2007). In the course of this research three rules have been proposed as serious contenders to the title of ES rule: the Relative Payoff Sum (RPS; Harley 1981), the Linear Operator (LOP; Bush and Mosteller 1955), and Perfect Memory (PM; Houston and Sumida 1987), the mathematical details of which are discussed in the methods.

Despite the considerable research effort devoted to ES learning rules, none have emerged as convincingly evolutionarily stable. Strong conclusions have been hampered by a combination of three major problems: first, few studies have pitted all rules against all others; second, all studies have used rules fitted with just a few parameter values, apparently chosen arbitrarily; third, almost all rules have been tested in unchanging environments where learning is of little value.

One of the most complete investigations into the question of ES learning rules has been conducted by Beauchamp (2000). To our knowledge, this is the only study that has attempted to study ES properties of learning rules in competition against each other. To do so, he used an agent-based model but tested rules using only three parameter values that were apparently chosen arbitrarily. Harley's 1981 original concern of whether a learning rule might lead a population to adopt an uninvadable strategy through behavioural means cannot be addressed without determining the parameters which drive these learning rules. To date all studies of the ES properties of learning rules have neglected the importance of the exact parameters used when testing the rule. Given the possible set of parameter values for these rules, only a miniscule portion of the available parameter space has been explored. If we are to conclude about a rule's evolutionary stability, it is imperative that we do so knowing that a rule's success is not just due to its being fitted with better-performing parameters. The only way to do this is by using each rule's optimal set of parameters.

How do we find optimal parameter values for these rules to use in testing? An analytical solution to these equations is out of reach, and the set of possible parameter values (the *parameter space*) is too large to feasibly conduct an exhaustive search. To solve this problem, we turn to a heuristic search technique known as a *genetic algorithm*. Genetic algorithms mimic the techniques of natural selection - differential reproduction, mutation, recombination - to find solutions to optimization problems (Sumida et al. 1990; Huse et al. 1999) Here, we use the genetic algorithm to evolve candidate rules with different parameter values, selecting those which perform best in the social foraging task to reproduce and using mutation and recombination to sweep the parameter space. One of the virtues of the genetic algorithm approach to modelling is that the evolution of traits can be made explicit (Hamblin and Hurd 2007; Ruxton and Beauchamp 2008), and by linking it to a model with an explicit description of a behavioural mechanism, insights into the interaction between the two may be gained (for a review, see (Seth 2007)). A cautionary note is required here, though, since the language of the field of evolutionary computation borrows heavily from biology while the comparisons between the two are not always so clear. It is important not to take the jargon of genetic algorithms too literally, as the details of the GA may seem odd, biologically; parameters and methods for genetic algorithms are usually chosen for search power, not biological realism (see Ruxton and Beauchamp 2008, for a discussion on the ways of conceptualizing genetic algorithms in behavioural ecology).

Beauchamp tested the properties of these rules as agents were engaged in playing one of two foraging games, the Producer-Scrounger game (Barnard and Sibly 1981) or an Ideal Free Distribution game (Fretwell and Lucas 1969; Sutherland 1983). Given that Beauchamp's results are similar whether the agents are engaged in a PS or an IFD game, we chose to have our agents play only a PS game. Although most experimental work on PS games concerns foraging in small flocks of birds (Giraldeau and Caraco 2000), it is important to realize that the structure of the PS game is more general and applies widely to any case where the investment of some individuals is exploited by others (Barnard 1984) much like the caller and silent satellite male strategies of many toads (e.g. Howard 1978) or the digging versus entering strategies of digger wasps (Brockmann et al. 1979).

As in all investigations of the ES property of learning rules, Beauchamp's (2000) study is set in an unchanging environment. This is problematical because learning may be of most value when the environment is at an intermediate level of variability

(Kerr and Feldman 2003; Stephens 1991). So testing a learning rule under conditions where learning is of little value may not have provided the rules with conditions that allowed them to perform efficiently. To provide rules with a variety of conditions we focus on changing two variables: group size, and environmental variability. Population size is relevant for both biological and technical reasons. Technically, genetic algorithms are more powerful with larger group sizes, since a large group (population) size means more candidate rules to select among. Biologically, we investigate the effect of group size to determine how the use of learning may change in large or small groups. With regards to environmental variability we will investigate rule performance as environmental features such as patch density and food items per patch.

Our first objective is to go beyond the use of arbitrary parameters when testing rules. To do this we determine the optimal parameters for each rule using a genetic algorithm. As this is occurring, the rules simultaneously compete with each other in the genetic algorithm, allowing us to form a clearer picture of the evolutionary stability of the rules, which is our second objective (Houston and Sumida 1987). Third, we wish to establish the evolutionary stability of rules in environments that vary. Finally, we hope to determine whether the rules predict similar or distinct group structures, that is whether agents will end up specializing on one or the other alternative or instead become generalist individuals that switch from one to the other alternative.

II.3 Methods

II.3.1 The model

We use an agent-based foraging model that builds on the model described in Beauchamp (2000) and extends it by using a genetic algorithm to optimize the rule type and rule parameter choices of the agents in the model.

The learning rules

Each rule has its own peculiarities. The RPS has two components: one concerns the estimated value of the alternatives, the other is a decision based on these values.

Relative Payoff Sum (RPS):

$$S_i(t) = x \cdot S_i(t-1) + (1-x) \cdot r_i + P_i(t) \tag{II.1}$$

where $S_i(t)$ is the value placed on behavioural alternative i at time t, x is the memory factor which determines how highly the past is valued, r_i is the *residual*, the cutoff below which the valuation of the alternative cannot go, and $P_i(t)$ is the payoff to the alternative during the current round (i.e. the amount of food eaten by the agent during that time step as above).

In essence, the estimated values of the alternatives are updated by experience using a memory factor to weight past against current information, and the residuals provide default values for each alternative in the absence of sampling.

The linear operator rule is the simplest of the three rules, and has been a popular choice for simulation and empirical work (Lefebvre 1983; Bernstein et al. 1988; Frischknecht 1996; Beauchamp and Fernández-Juricic 2004; Amano et al. 2006). The form of the linear operator rule is:

Linear Operator (LOP):

$$S_i(t) = x \cdot S_i(t-1) + (1-x) \cdot P_i(t) \tag{II.2}$$

where the variables are the same as for the RPS rule.

The linear operator rule differs from the RPS rule mainly in its lack of a residual value. This means that, unlike the RPS rule, if an alternative stops paying off, the value that is placed on the alternative can go to zero. The other difference is that in the LOP rule, the memory factor influences the contribution of the payoff to the value placed on the alternative.

The perfect memory rule assumes the animal retains knowledge of all payoffs up until the current time step. Thus, the value placed on an alternative is a ratio of the total payoffs for that alternative to the total payoffs for all alternatives. Unlike the RPS or LOP rules, there is no memory factor to devalue older experience in favour of more recent experience.

Perfect Memory (PM):

$$S_i(t) = (\alpha + R_i(t))/(\beta + N_i(t)) \tag{II.3}$$

where α and β are parameters, $R_i(t)$ is the total payoffs to alternative i since the first time step to time t and $N_I(t)$ is the total payoff to the player from all alternatives from the first time step to time t.

The parameters α and β are constant parameters with no immediately obvious interpretation.

Foraging simulation

Agents played a producer-scrounger foraging game (Barnard and Sibly 1981) on a variable-sized grid arranged into s_x by s_y patch sites where 20% of the patches actually contain food at the beginning of the simulation. Similarly, the group size of agents (n_{agents}) was set to 10% of the area of the grid. We simulated 20 runs each for grid sizes of { 10x10, 20x20, 30x30, 40x40, 60x60, 100x100 } leading to group sizes of { 10, 40, 90, 160, 360, 1000 }. Patches contained 20 food items.

At each time step, agents played either producer or scrounger. If they played producer, they would search for a food patch at their immediate location, with discovery being assured if food was present. If no food was found, they would move one square in one of the four cardinal directions (up, down, left, right), and select their strategy again. Agents could either move or eat in a single time step, not both. If agents played scrounger, they would scan the entire grid for conspecifics exploiting a patch and move towards the nearest feeding conspecific to join the discovery (if one was found). Scroungers chose the patch to move to only as a function of distance, regardless of the number of foragers at each patch. Agents moving to scrounge at a patch moved at twice the rate of movement while searching, or two grid squares per turn. If no conspecifics exploiting a patch were detected anywhere on the grid, agents would move randomly as above and select their strategy again. Agents exploiting a patch, whether as a producer or scrounger, would continue feeding at the rate of one food item per turn until the food was depleted. If the number of agents feeding at a patch exceeded the food available at the patch, agents would be selected randomly to consume the final food items. Upon depletion, the patch would be recreated at a random point elsewhere on the grid to maintain the overall patch density. There is no difference in energy consumption between the alternatives, and to simplify Beauchamp's analysis, we ignored the effect of forager interference by setting it to zero.

Agents used one of three learning rules specified in the introduction, as encoded in their genetic algorithm chromosome (see next section) to determine their allocation to searching as a producer or scrounger. At the end of each time step, agents updated their value for producer and scrounger based on the results of that time step, and recalculated p, the probability of playing scrounger. p was calculated according to one of two possible equations:

$$\text{Matching: } p = \frac{S_s(t)}{S_s(t) + S_p(t)}, \text{ or} \tag{II.4}$$

$$\text{Maximizing:} p = \begin{cases} 1 & \text{if } S_s > S_p \\ 0 & \text{otherwise} \end{cases} \tag{II.5}$$

This equations follow the usage in Beauchamp (2000), which is itself common (e.g. Groß et al. 2008).

When the probability of scrounging had been calculated, the time step was considered completed and the process would begin again. Agents foraged for $t_{\text{sim}} = 500$ iterations, after which the foraging game ended.

The genetic algorithm

After the simulation component was finished, fitness values (calculated from the feeding rates) were fed to the genetic algorithm. Agents were ranked by their fitness values and selected for reproduction as follows: the bottom 10% of fitness "died", and therefore did not reproduce, while individuals in the top 10% of fitness values were eligible to replace the bottom 10%. Selection from the top 10% was proportional to fitness values, where individuals with higher fitness values had a higher chance of being chosen ("roulette wheel" selection; Goldberg 1989; Lee and Kim 2005). Because the members of the top 10% were sampled with replacement, a given individual in the top 10% could be selected more than once for replacement of the bottom 10%.

Once selection was finished, the selected group bred a new generation through the genetic operators of crossover and mutation, which are used to introduce variation into the new group of agents. Pairs of haploid "parents" were chosen for breeding, and would undergo a uniform crossover operation, in which each locus is swapped between the parents with probability $p_c = 0.5$ (Goldberg 1989; Lee and Kim 2005). To clarify, each of the nine loci (see below) in the parent's chromosome were taken in turn, and if a randomly generated number between 0 and 1 was less than 0.5, the values of the loci were swapped between the parents; thus, on average 4.5 loci would be swapped between each set of parents. After swapping loci, the two new "child" chromosomes were subjected to mutation, with a per-locus probability of $p_m = 0.002$ (see Table II.1 for the bounds placed upon mutation), and the "children" were placed in the new group. This was continued until a new group the same size as the old group was constructed (group size was constant). With selection and reproduction completed, the foraging game was restarted with the new group. This cycle continued to $t_{\text{ga}} = 500$ iterations of the genetic algorithm.

A nine-locus chromosome determined an agent's choice of learning rule (Table II.1). The first locus coded for rule choice 1,2,3 for RPS, LOP, and PM respectively, and the remaining eight loci coded for the parameters to each rule. Loci 2, 3, and 4 coded for the RPS parameters r_{producer}, x, and $r_{\text{scrounger}}$ respectively. Loci 5 and 6 coded for the LOP memory factor x and the choice of matching or maximizing algorithm, while Loci 7, 8, and 9 coded for the PM parameters α and β and choice of matching or maximizing algorithms (the RPS rule used only matching, following Beauchamp (2000)). Table II.1 summarizes the chromosome as well as the bounds placed upon mutation. The parameter values for the learning rule encoded into the agent's chromosome in the first generation were randomly selected, and optimized by the genetic algorithm in following generations. To determine if a group had fixated on a particular strategy, we used an operational definition of a stable group with an average of over 90% dominance by one strategy for at least the last 100 generations (an average was used to handle the problem of mutation noise at small grid sizes).

Locus	Description	Range	Mutation Bounds
1	Rule type	$\{x \mid x \in [1,2,3]\}$	$\{m \mid m \in [1,2,3]\}$
2	RPS producing residual.	$\{x \in \mathbb{R}^+ \mid x \geq 0\}$	$\{m \in \mathbb{R} \mid m \in [-1.0, 1.0]\}$
3	RPS memory factor.	$\{x \in \mathbb{R}^+ \mid 0 \leq x \leq 1\}$	$\{m \in \mathbb{R} \mid m \in [-0.1, 0.1]\}$
4	RPS scrounging residual.	$\{x \in \mathbb{R}^+ \mid x \geq 0\}$	$\{m \in \mathbb{R} \mid m \in [-1.0, 1.0]\}$
5	LOP memory factor.	$\{x \in \mathbb{R}^+ \mid 0 \leq x \leq 1\}$	$\{m \in \mathbb{R} \mid m \in [-0.1, 0.1]\}$
6	LOP scrounge algorithm.	$\{x \mid x \in [\text{maximize}, \text{match}]\}$	$\{m \mid m \in [\text{maximize}, \text{match}]\}$
7	PM α parameter.	$\{x \in \mathbb{R}^+ \mid x \geq 0\}$	$\{m \in \mathbb{R} \mid m \in [-10.0, 10.0]\}$
8	PM β parameter.	$\{x \in \mathbb{R}^+ \mid x \geq 0\}$	$\{m \in \mathbb{R} \mid m \in [-10.0, 10.0]\}$
9	PM scrounge algorithm.	$\{x \mid x \in [\text{maximize}, \text{match}]\}$	$\{m \mid m \in [\text{maximize}, \text{match}]\}$

Table II.1: Genetic algorithm chromosome description.

The code for the genetic algorithm is based on that used and validated previously in Hamblin and Hurd (2007), rewritten in Python (Lee and Kim 2005; Bassi 2007). The source code is available from the authors upon request.

Environmental variability

Frequency-dependent variability is a natural component of the model, but environmental variability must be explicitly added in. To do so, we performed a series of test runs which held group size constant but varied environmental parameters (patch density and patch richness) that might have had an effect on the proportion of scrounger use, which is the response variable of interest in demonstrating an effect on forager behaviour. Preliminary analysis showed that the effect of patch density on scrounger use was markedly greater than that of patch richness, with patch density defined as the number of patches on the grid. This effect was qualitatively the same regardless of group size used for the test. Environmental variability was therefore added to the model by modifying patch density N times throughout the foraging simulation to create $N+1$ environments with different patch densities experienced by the agents. Patch density would start at 20% and then new patch densities were drawn from a uniform distribution from 1% to 10%, which was the range identified as having the maximum effect on scrounger proportion; thus, runs done with $N = 0$ are comparable to runs done without environmental variability. We then performed runs with different values of N, with increasing values of N representing greater environmental variability. For the results presented here we varied N from 0 to 9; we tested higher values of N, which had no effect on the pattern of results. 20 runs were done at each level of environmental variability, at a group size of 90.

II.4 Results

II.4.1 Base model

The RPS rule usually drives to fixation in under 100 generations (Figure II.1). From table II.2, it is clear that RPS is the dominant rule, evolving to fixation with increasing probability as the group size increases; this probability is also considerably larger than either of the other two rules.

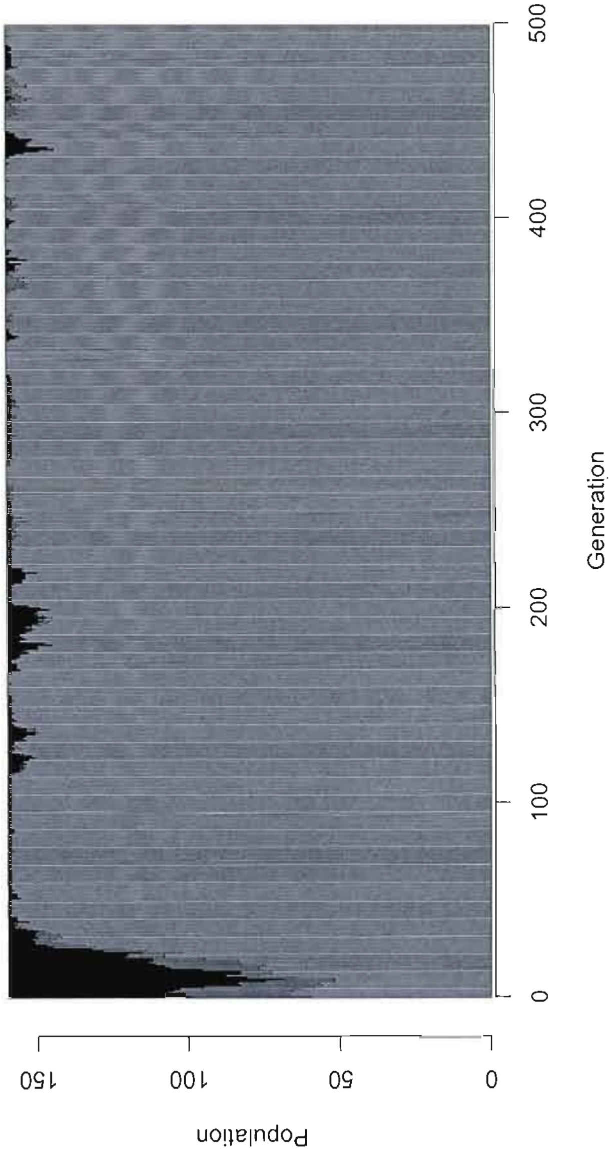

Figure II.1: Typical evolution of learning rules in agents playing a producer-scrounger game over 500 generations of discrete time. This run was done at a grid size of 40x40 with 160 agents and 320 food patches with 20 items in each patch. The bars indicate the proportion of the group playing a strategy (light grey is Relative Payoff Sum, dark grey is Linear Operator, black is Perfect Memory).

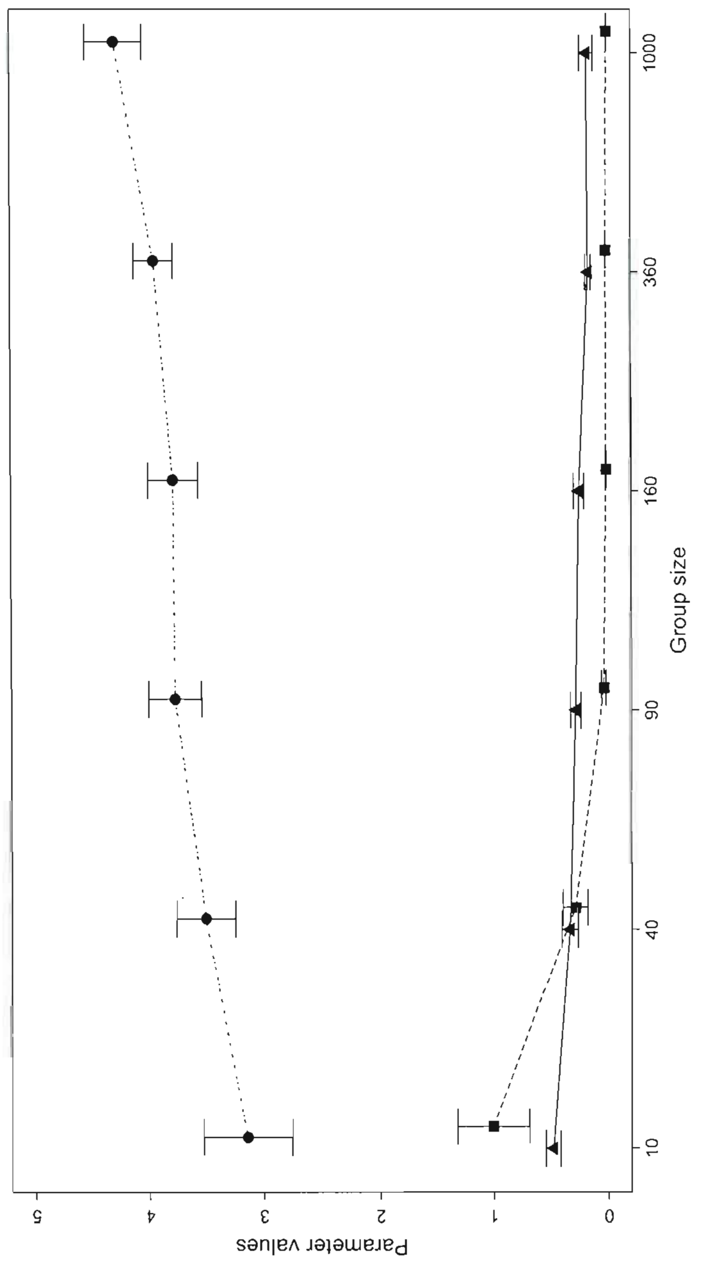

Figure II.2: Mean optimal parameter values selected for by the genetic algorithm with standard errors for the RPS rule as group size increases. Circles are producer residuals, triangles are memory factor values, and squares are scrounger residuals.

	Fixation:			
Group Size (n)	RPS	LOP	PM	None
10 (20)	60%	15%	20%	5%
40 (20)	70%	0%	15%	15%
90 (20)	95%	0%	5%	0%
160 (20)	95%	0%	5%	0%
360 (20)	100%	0%	0%	0%
1000 (5)	100%	0	0	0

Table II.2: The percentage of runs in which each of the three learning rules, relative payoff sum (RPS), linear operator (LOP), and perfect memory (PM) went to fixation for each group size tested. Due to computational constraints, only 5 runs at the group size of 1000 were done.

The parameters of the RPS rule evolved as a function of the group size provided (Figure II.2). The parameter for the residual associated with producer increased with the group size while the parameter for the residual associated with scrounger declined and remained low over a wide range of group sizes. The parameter coding for the memory factor also declined with group size. For the memory factor and scrounger residual, the standard deviation decreases as the group size increases and although no single value is ever settled upon, the two parameters appear to be approaching some typical value, while the producer residual remains more variable. More importantly, the parameter for the producer residual is always significantly higher than the parameter for the scrounger residual. Since the other rules were selected out quickly and only fixated in a small number of runs, drawing conclusions about their parameter values would be difficult since we can not know whether the rule was selected out in a particular run because it did not achieve optimal parameter values or because it achieved those values but still lost to another, superior rule (fixation at group sizes greater than 10 occurred rarely enough to give us confidence that the PM and LOP rules are local, not global, optima) . We performed enough runs that the LOP and PM rules were nearly certain to achieve optimal values often enough to give us confidence about the attractiveness of the RPS rule, but for these reasons interpreting LOP and PM parameter values would be difficult, and so we focus here on the values of the RPS parameters.

We found a pattern of increasing specialization as group size increases (Figure II.3).

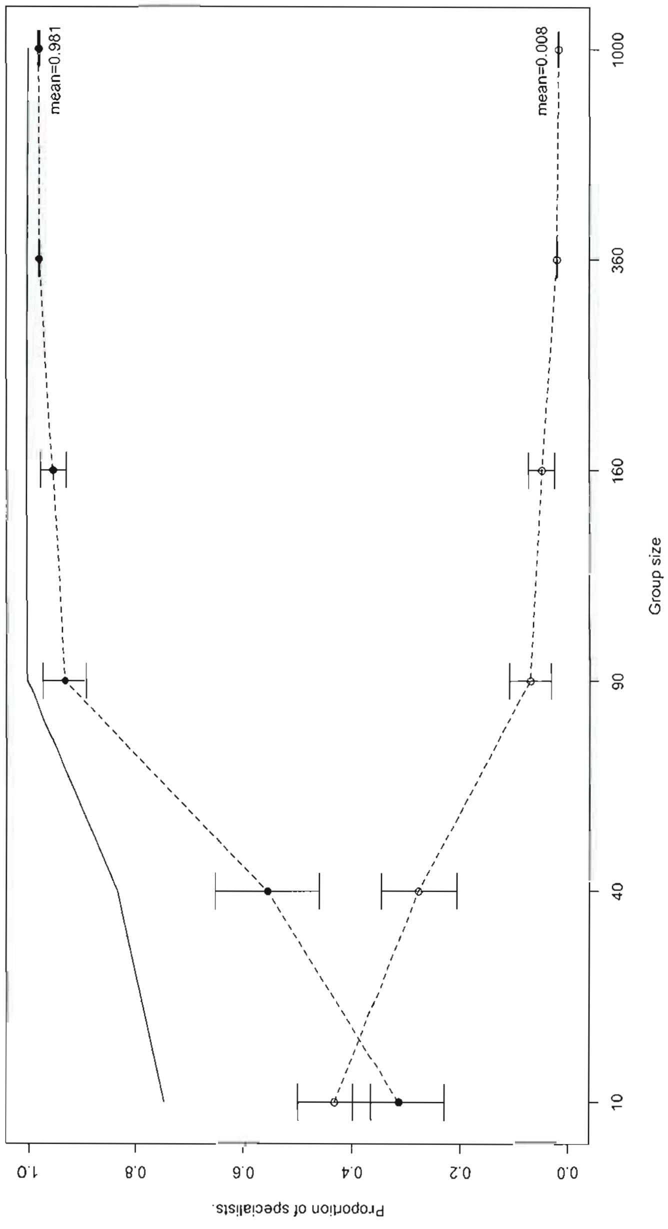

Figure II.3: Mean proportion of individuals that are specialist producers (filled circles) or scroungers (open circles) as a function of group size. Means are based on 20 runs and bars show standard errors. The solid line is the combined mean of specialists.

II.4.2 Environmental variability

Table II.3 shows the trend in rule evolution as a function of environmental variability and group size. Group size was the only significant predictor of fixation when entered into a logistic regression of size, variability, and their interaction against a binary response (1 = RPS, 0 = the other 3 outcomes; size: $z_{796} = 6.533$, $p < 0.00001$; variability: $z_{796} = -0.201$, $p = 0.84$; interaction: $z_{796} = -1.838$, $p = 0.07$). The genetic algorithm evolved the RPS rule to fixation preferentially for group sizes greater than 10. RPS parameter evolution seemed to be unresponsive to environmental variability (Figure II.4 - note the similarity to Figure II.2).

As before, we also examined the pattern of specialization, this time as a function of increasing environmental variability. Specialization increased with increasing environmental variability (Figure II.5), and examining producer and scrounger specialists separately shows that producer specialists increase as the environment becomes more variable (Figure II.5). Also as before, the parameter for the producer residuals were consistently an order of magnitude greater than the parameter for the scrounger residuals.

II.5 Discussion

Our results show a clear trend amongst the three learning rules that we tested: the RPS rule evolves to fixation with increasing frequency as the group size increases, and evolves to fixation at a minimum of 60% at the smallest group sizes. The evolutionary stability of the RPS learning rule that we found confirms an earlier analytical analysis by Tracy and Seaman Jr. (1995) which showed that RPS was an ES learning rule. The genetic algorithm provides evidence for the stability of RPS, though it does not conclusively demonstrate that the LOP or PM rules are not evolutionarily stable, just that RPS is a much more powerful attractor in the strategy space, likely because it converges faster to the ESS (Tracy and Seaman Jr. 1995). Harley's (1981) original concern of whether a learning rule might lead a group to adopt an uninvadable strategy through behavioural means cannot be addressed without determining the parameters which drive these learning rules. To date all studies of the ES properties of learning rules have neglected the importance of the exact parameters used when testing the rule. Our study is the first to provide support for the ES property of

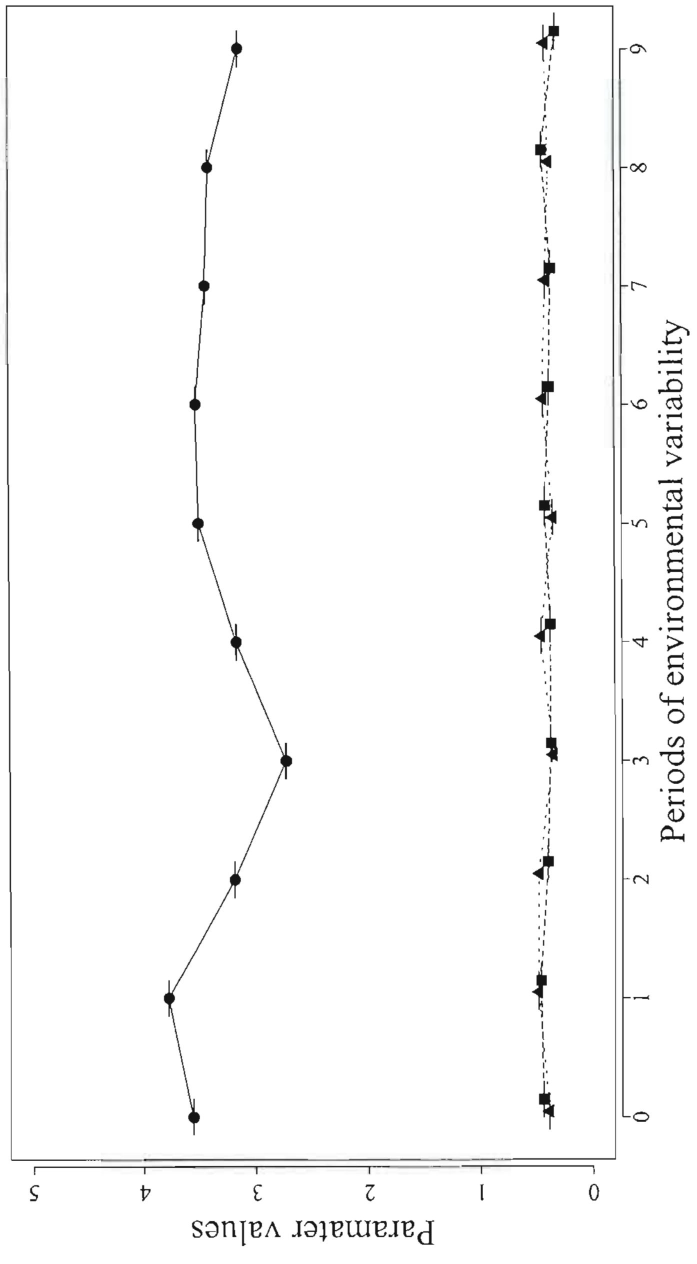

Figure II.4: Mean optimal parameter values selected for by the genetic algorithm with standard errors for the RPS rule as group size increases. Circles are producer residuals, triangles are memory factor values, and squares are scrounger residuals. Variability increases to the right, and runs are done at group size 90. Means are based on 20 runs.

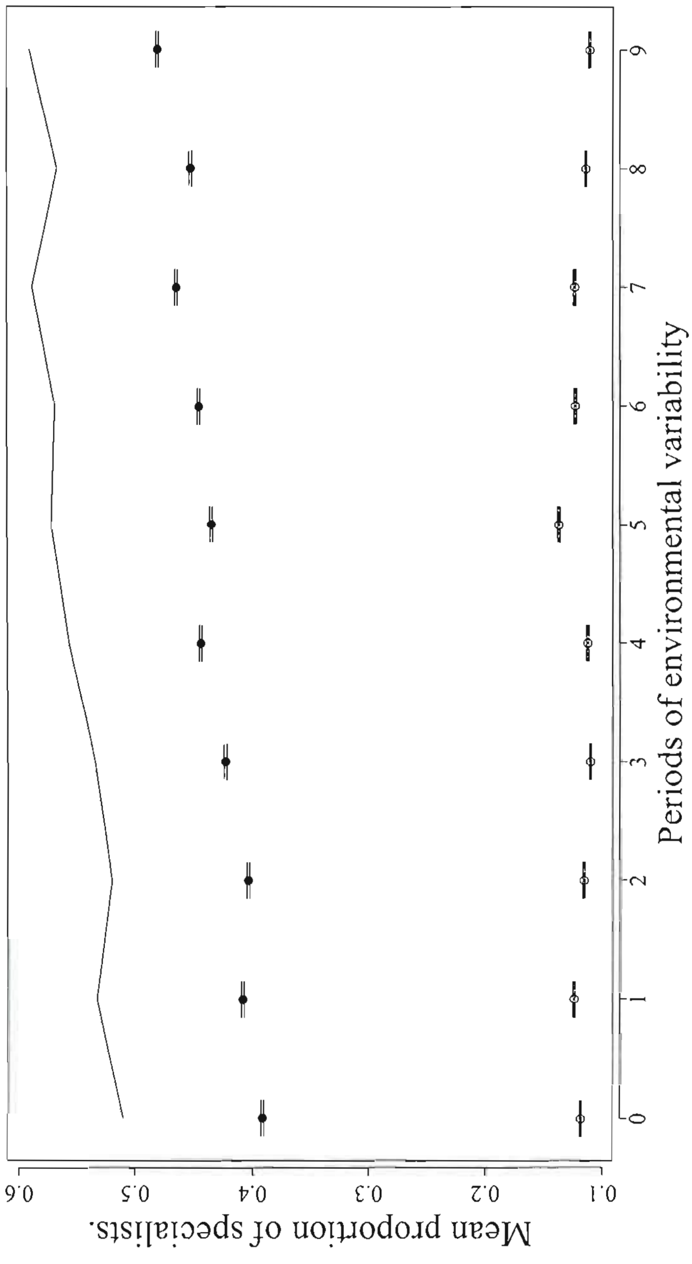

Figure II.5: Mean proportion of individuals that are specialists as a function of environmental variability. Specialist producers are filled circles, specialist scroungers are open circles, and the line shows the trend in combined specialization. Means are based on 20 runs and bars show standard errors; variability increases to the right. Runs done at a group size of 90.

[Group size 10]

	Periods of variability:									
Rule	0	1	2	3	4	5	6	7	8	9
RPS	60%	35%	35%	25%	30%	30%	5%	25%	40%	30%
LOP	0%	0%	5%	0%	0%	0%	0%	0%	0%	0%
PM	30%	40%	35%	50%	35%	30%	75%	40%	45%	55%
None	10%	25%	25%	25%	35%	40%	20%	35%	15%	15%

[Group size 40]

	Periods of variability:									
Rule	0	1	2	3	4	5	6	7	8	9
RPS	95%	90%	100%	95%	60%	70%	65%	80%	30%	80%
LOP	0%	5%	0%	0%	0%	0%	0%	5%	10%	10%
PM	0%	0%	0%	0%	0%	0%	0%	0%	0%	0%
None	5%	5%	0%	5%	40%	30%	35%	15%	65%	10%

[Group size 90]

	Periods of variability:									
Rule	0	1	2	3	4	5	6	7	8	9
RPS	100%	95%	100%	95%	100%	90%	95%	95%	90%	85%
LOP	0%	5%	0%	0%	0%	0%	0%	0%	0%	0%
PM	0%	0%	0%	0%	0%	0%	0%	0%	0%	0%
None	0%	0%	0%	5%	0%	10%	5%	5%	10%	15%

[Group size 160]

	Periods of variability:									
Rule	0	1	2	3	4	5	6	7	8	9
RPS	100%	100%	100%	100%	100%	100%	100%	100%	100%	100%
LOP	0%	0%	0%	0%	0%	0%	0%	0%	0%	0%
PM	0%	0%	0%	0%	0%	0%	0%	0%	0%	0%
None	0%	0%	0%	0%	0%	0%	0%	0%	0%	0%

Table II.3: Rule evolution by group size and environmental variability. $n = 20$ runs were done for each combination of group size and variability.

the RPS while allowing candidate rules to evolve to their optimal parameter values.

Our finding of a single learning rule with great attractive power in the strategy space somewhat contradicts simulation results of Beauchamp (2000), who instead reported multiple stable rules. However, this contradiction may be attributed to use of a single, rather small, group size of 10 foragers where Beauchamp's results are in line with ours. We found that as the group size increases the other rules can no longer evolve to fixation. The overwhelming stochasticity of the payoffs that are expected at such a small group size makes the fitness landscape almost impossible to optimize because any change in behaviour by one individual will exert a strong influence on the payoffs obtained by all other individuals in the group. As the group size increases the variance in payoffs decreases and the genetic algorithm is better able to reach fitness optimums. If we are correct that small group sizes make it more difficult to reach the optimal allocation to producer and scrounger, then both experimental work and field observations of Producer-Scrounger systems (Mottley and Giraldeau 2000; Wu and Giraldeau 2005), should find that using larger groups increases the rate at which animals reach behavioural equilibria. No such study has yet been conducted. Our result also suggests that in animals confined to frequency-dependence in small groups of 10 or less, any of the three learning rules or perhaps combinations of these ought to be expected. To date no study has explored whether populations are polymorphic for learning rules.

Why does the RPS rule predominate at any but the smallest group sizes? The answer may lie in the structure of the learning rules themselves. The linear operator rule allows for adjustment to rapidly changing local conditions, but cannot continue sampling an alternative once that has failed to pay off for any appreciable amount of time. In other words once one alternative is lost there is no real way of allowing the animal to sample it in case its value suddenly increased. The perfect memory rule accumulates information about all the payoffs ever received for an alternative which creates an important inertia of responding that prevents the animal from taking advantage of rapid changes in the value of alternatives. The RPS presents some important advantages over those two rules. Because it incorporates parameters for residuals, constant parameters that fix the lowest possible rate of responding to each behavioural alternative, neither of these alternatives can ever totally extinguish. The animal will always have a non-zero probability of trying an alternative even if it hasn't paid off for a long time. Moreover, the memory parameter weighs the importance of past events such that the inertia provided by the past can be small. Finally, the mathematical structure of the rules themselves may give the RPS rule an advantage, since the RPS rule has one extra parameter and a model's performance increases with the number of parameters in the model. This should not, however, be taken as a definite cause for why the RPS was selected by the genetic algorithm in preference to the other rules, since the increased number of parameters also makes for a more difficult optimization problem to solve in the first place. In short, the number of parameters may have helped the RPS rule perform better in the foraging game, but may have disadvantaged it in the genetic algorithm, and it is unclear which effect would be more important.

The genetic algorithm allows the parameters of all the learning rules to evolve to optimal values. The evolution of parameter values shows an interesting pattern: at all group sizes, the RPS's parameter for the producing residual evolves to a much greater value than the equivalent parameter for scrounging. This makes sense and demonstrates that it is optimal never to give up the producer strategy even if it temporarily fails to provide rewards. It is not the same, however, for the scrounger strategy which is associated with a much lower residual value. This implies that it can pay to stop scrounging altogether when current payoffs are low, only to be reacquired when scrounging begins to pay off again (since the parameter for the scrounging residual approaches, but does not reach, zero, which forces the payoff to be sampled occasionally). This asymmetry in residual values means that when small groups of animals are engaged in a producer-scrounger game, if they are using the RPS rule they need not try to determine a combination of producing and scrounging. They should instead start off with a low level of scrounging and increase its use when the payoffs it obtains from that option are relatively greater than those from producer. The RPS with a higher producing residual therefore makes learning the equilibrium use of producer and scrounger much easier. On the other hand, an RPS with a memory factor very close to zero can actually inhibit changing behaviour, such that the ratio of the residuals is the overriding factor in the decision whether to play producer or scrounger; in this case, evolution would be required to shift the ratio of producer and scrounger behaviours; the interplay between these elements of the RPS rule may help regulate population dynamics (Coolen et al. 2007).

This discrepancy in residuals between the two tactics is likely to be a factor in the pattern we observed for the structure of the groups which evolved playing the RPS rule. We found that tactic specialization (playing a pure strategy of producer or scrounger) increased with group size. This move from a monomorphic group playing a mixed behavioural strategy to a dimorphic group playing fixed producing or scrounging has interesting implications for foraging groups. The instability of mixed strategies in large, learning populations has been predicted analytically (e.g. Crawford 1989), while evidence of mixed strategy use is common in empirical work, which typically uses small group sizes (Giraldeau and Dubois 2008). The work we present here on learning rules may represent a bridge between these two approaches.

Finding a test for the RPS rule which distinguishes it from other rules (such as the linear operator rule) has proven difficult in the past (e.g. Regelmann 1984; Milinski 1984; Kacelnik and Krebs 1985). This difference in the producing and scrounging residuals suggests an easy empirical test of the RPS rule. If the parameter for the producing residual is much higher than the parameter for the scrounging residual, then it should be much easier to reduce scrounging behaviour to lower levels than producing behaviour in animals that are using the RPS rule; if producing is maintained at a high level despite its failing to payoff, this would provide evidence against the LOP and PM rules, since neither has a parameter for residuals to keep an animal's sampling of producing from waning after it fails to payoff for a substantial period of time. The ease of scrounging has been demonstrated empirically (Coolen et al. 2001), but we are unaware of any test which has attempted to determine the relative difficulty of manipulating the producer and scrounger use of an animal. The predominance of RPS for most group sizes also has important implications for empirical work on learning, since many of the studies which have been done to date have used the linear operator rule as a reference point (Lefebvre 1983; Bernstein et al. 1988; Frischknecht 1996; Amano et al. 2006), probably because of its relative simplicity, but our results show that this may be incorrect.

The evolution of parameter values showed not only that the residuals evolved a definite pattern, but that the memory factor for the RPS rule was selected to be reduced (approaching, but not reaching zero). This means that optimal RPS parameters were selected to discount recent information gained about the environment. Taken together, the optimal residuals and memory factor generate an RPS that is rather insensitive to short-term changes in payoffs but whose overall level of using strategies is fixed by the residuals. The values of the residuals represent an inflexible bias for producing and scrounging that leaves little room for local adjustment. This is rather paradoxical because there is an optimal ES learning rule that evolves towards parameters that place greater weight on genetically determined fixed residuals and reduces the importance of experience by having a small memory factor; in essence, the optimal learning rule rejects learning.

In our study the payoffs associated with producing and scrounging varied as a result of two distinct processes. First, the adjustment in individual use of producing and scrounging as foraging progressed changed the payoffs experienced by the other players. Second, we changed the resource distribution over time which affected equilibrium levels of producing and scrounging, and found that highly stochastic environments should select against learning. The RPS evolved parameters that forced genetically fixed producing at high levels, suggesting that the payoffs may simply be too stochastic to be worth tracking. Intermediate levels of environmental variation that would lead non-social foraging theorists to expect selection for learning (Kerr and Feldman 2003; Stephens 1991) may in fact select against learning in a social foraging context, as it did in this study, where no amount of environmental variation evolved a rule that emphasized short-term flexibility. The RPS rule, with its combination of flexible memory factor and hard-coded residual values, was apparently best able to deal with the trade-off between the advantage of learning to respond to new circumstances and the ability to pre-select for the best average response over multiple environments.

The finding that the RPS rule evolves to ignore short-term experience in favor of genetically fixed behaviour is surprising, and suggests that our picture of the value that learning brings to an organism is incomplete. Given that our model includes both frequency-dependent and environmental variation, we can only ask whether our model has failed to capture some relevant component of a learning response to one or both of those sources of variation, or if these kinds of uncertainty are not what drives the acquisition and maintenance of learning ability. Answering that question will be an important step in understanding the role of learning in animal behaviour.

It remains to be seen, however, whether the RPS generalizes to other behavioural decision situations such as the evolution of cooperation or the ideal-free distribution. Future work should therefore test this rule against other game theory models. Frequency-dependent effects on learning evolution at small group sizes also deserves more attention than could be paid here; given its relevance to natural situations, where small groups may be common, it is important to determine if the genetic algorithm's lack of agreement on rule evolution is just noise or if a pattern can be found. Finally, since the rule structure itself is an arbitrary creation, we are currently using genetic programming techniques to evolve not only the parameters to the rules, but the structure of the rules themselves.

The RPS rule is clearly a superior learning rule at all but the smallest group sizes in a foraging producer-scrounger game, and the evolved form of the rule, with its emphasis on fixed residuals in the face of both frequency-dependent and environmental variation, raises important questions about animal learning in a social foraging context. The relative payoff sum may therefore provide a single rule that accounts for the way an animal's ecology comes to affect its specific set of learning sensitivities.

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II.7 Bibliography

Amano, T., Ushiyama, K., Moriguchi, S., Fujita, G., and Higuchi, H. (2006). Decision-making in group foragers with incomplete information: Test of individual-based model in geese. *Ecological Monographs*, 76(4):601–616.

Barnard, C. J. (1984). *Producers and scroungers : Strategies of exploitation and parasitism.* Chapman & Hall, London.

Barnard, C. J. and Sibly, R. M. (1981). Producers and scroungers: A general model and its application to captive flocks of house sparrows. *Animal Behaviour*, 29:543–550.

Bassi, S. (2007). A primer on python for life science researchers. *PLoS Computational Biology*, 3(11):2052–2057.

Beauchamp, G. (2000). Learning rules for social foragers: Implications for the producer-scrounger game and ideal free distribution theory. *Journal of Theoretical Biology*, 207:21–35.

Beauchamp, G. (2004). On the use of public information by social foragers to assess patch quality. *Oikos*, 107(1):206–209.

Beauchamp, G. and Fernández-Juricic, E. (2004). The group-size paradox: Effects of learning and patch departure rules. *Behavioral Ecology*, 16(2):352–357.

Beggs, A. W. (2005). On the convergence of reinforcement learning. *Journal of Economic Theory*, 122:1–36.

Bernstein, C., Kacelnik, A., and Krebs, J. R. (1988). Individual decisions and the distribution of predators in a patchy environment. *Journal of Animal Ecology*, 57(3):1007–1026.

Brockmann, H. J., Grafen, A., and Dawkins, R. (1979). Evolutionarily stable nesting strategy in a digger wasp. *Journal of Theoretical Biology.*, 77:473–496.

Bush, R. and Mosteller, F. (1955). *Stochastic models for learning.* New York. Wiley.

Coolen, I., Giraldeau, L.-A., and Lavoie, M. (2001). Head position as an indicator of producer and scrounger tactics in a ground-feeding bird. *Animal Behaviour*, 61:895–903.

Coolen, I., Giraldeau, L.-A., and Vickery, W. L. (2007). Scrounging behavior regulates population dynamics. *Oikos*, 116:533–539.

Crawford, V. P. (1989). Learning and mixed-strategy equilibria in evolutionary games. *Journal of Theoretical Biology*, 140(4):537–550.

Dugatkin, L. A. and Reeve, H. K. (1997). *Game theory and animal behavior.* Oxford University Press.

Fretwell, S. D. and Lucas, H. L. (1969). On territorial behavior and other factors influencing habitat distribution in birds: I. theoretical development. *Acta Biotheoretica*, 19(1):1–36.

Frischknecht, M. (1996). Predators choosing between patches with standing crop: the influence of switching rules and input types. *Behavioural Ecology and Sociobiology*, 38:159–166.

Giraldeau, L.-A. and Caraco, T. (2000). *Social Foraging Theory.* Monographs in Behavior and Ecology. Princeton University Press, New Jersey.

Giraldeau, L.-A. and Dubois, F. (2008). Social foraging and the study of exploitative behaviour. in press.

Goldberg, D. E. (1989). *Genetic algorithms in seach, optimization, and machine learning.* Addison-Wesley, Reading, Massachusetts.

Groß, R., Houston, A. I., Collins, E. J., McNamara, J. M., Dechaume-Moncharmont, F.-X., and Franks, N. R. (2008). Simple learning rules to cope with changing environments. *Journal of the Royal Society Interface.*, 5:1193–1202.

Hamblin, S. and Hurd, P. L. (2007). Evolution's strategies: Genetic algorithms and game theory models. *Animal Behaviour*, 74(4):1005–1018.

Harley, C. B. (1981). Learning the evolutionarily stable strategy. *Journal of Theoretical Biology*, 89:611–633.

Harley, C. B. (1983). When do animals learn the evolutionarily stable strategy? *Journal of Theoretical Biology*, 105:179–181.

Harley, C. B. (1987). Learning rules, optimal behaviour, and evolutionary stability. *Journal of Theoretical Biology*, 127:377–379.

Hines, W. and Bishop, D. T. (1983). On learning and the evolutionarily stable strategy. *Journal of Applied Probability*, 20(3):689–695.

Houston, A. I. (1983). Comments on "learning the evolutionarily stable strategy". *Journal of Theoretical Biology*, 105:175–178.

Houston, A. I. and Sumida, B. H. (1987). Learning rules, matching, and frequency dependence. *Journal of Theoretical Biology*, 126:289–308.

Howard, R. D. (1978). The evolution of mating strategies in bullfrogs, *rana catesbeiana. Evolution*, 32:850–871.

Huse, G., Strand, E., and Giske, J. (1999). Implementing behaviour in individual-based models using neural networks and genetic algorithms. *Evolutionary Ecology*, 13:469–483.

Kacelnik, A. and Krebs, J. R. (1985). Learning to exploit patchily distributed food. In Sibly, R. M. and Smith, R. H., editors, *Behavioural Ecology. Ecological Consequences of Adaptive Behaviour*, pages 63–87. Blackwell Scientific Publications, Oxford.

Kerr, B. and Feldman, M. W. (2003). Carving the cognitive niche: Optimal learning strategies in homogeneous and heterogeneous environments. *Journal of Theoretical Biology*, 220:169–188.

Lee, W. and Kim, H.-Y. (2005). Genetic algorithm implementation in python. *Proceedings of the Fourth Annual ACIS International Conference on Computer and Information Science*, 2005:8–12.

Lefebvre, L. (1983). Equilibrium distribution of feral pigeons at multiple food sources. *Behavioural Ecology and Sociobiology*, 12:11–17.

Maynard Smith, J. (1982). *Evolution and the Theory of Games*. Cambridge University Press, New York, NY.

Milinski, M. (1984). Competitive resource sharing: An experimental test of a learning rule for esss. *Animal Behaviour*, 32:233–242.

Mottley, K. and Giraldeau, L.-A. (2000). Experimental evidence that group foragers can converge on predicted producer-scrounger equilibria. *Animal Behaviour*, 60:341–350.

Regelmann, K. (1984). Competitive resource sharing: A simulation model. *Animal Behaviour*, 32:226–232.

Ruxton, G. D. and Beauchamp, G. (2008). The application of genetic algorithms in behavioural ecology, illustrated with a model of anti-predator vigilance. *Journal of Theoretical Biology*, 250:435–448.

Seth, A. K. (2007). The ecology of action selection: Insights from artificial life. *Philosophical Transactions of the Royal Society, Biological Sciences*, 362:1545–1558.

Shettleworth, S. J., Krebs, J. R., Stephens, D. W., and Gibbon, J. (1988). Tracking a fluctuating environment: A study of sampling. *Animal Behavior*, 36:87–105.

Spataro, T. and Bernstein, C. (2007). Influence of environmental conditions on patch exploitation strategies of parasitoids. *Behavioral Ecology*, 18:742–749.

Stephens, D. W. (1991). Change, regularity, and value in the evolution of animal learning. *Behavioral Ecology*, 2(1):77–89.

Sumida, B. H., Houston, A. I., McNamara, J. M., and Hamilton, W. D. (1990). Genetic algorithms and evolution. *Journal of Theoretical Biology*, 147:59–84.

Sutherland, W. J. (1983). Aggregation and the 'ideal free' distribution. *The Journal of Animal Ecology*, 52(3):821–828.

Tracy, N. D. and Seaman Jr., J. W. (1995). Properties of evolutionarily stable learning rules. *Journal of Theoretical Biology*, 177:193–198.

Wu, G.-M. and Giraldeau, L.-A. (2005). Risky decisions: a test of risk sensitivity in socially foraging flocks of lonchura punctulata. *Behavioural Ecology*, 16(1):8–14.

CHAPTER III

COEVOLUTION OF SOCIAL INFORMATION USE

Preamble

This chapter presents an article published in the journal *Oikos* (Vol. 119, pp. 286-291). SH, KM, JMF, JN, GR, LAG developed the initial research question; SH developed the simulation with input from the other authors, performed the work, analyzed data, produced the figures, and wrote the methods section of the paper; JN added the time series analysis; all authors collaborated on the rest of the text.

Predator inadvertent social information use favours reduced clumping of its prey.

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III.1 Abstract

When animals forage socially, individuals can obtain prey from their own searching (producer tactic) or by using the behaviour of others (scrounger tactic) when it provides inadvertent social information (ISI) that food has been located. This ISI may either indicate the location of food (social information, SI), or it may indicate the quality of the resource (public information, PI). To date, few studies have explored the selective consequences for prey of being exploited by predators that use ISI. Prey exploited by such predators should evolve traits that favour high levels of ISI use (scrounging) because this would result in lower predator search efficiency given that fewer predators would be searching directly for the prey. Our simulations confirm that ISI-using predators should increase their use of ISI when their prey form larger clumps resulting in higher prey survival. Our objective therefore is to explore whether prey will evolve towards higher clumpiness when their predators use ISI, using genetic algorithm simulation. The prey were subjected to one of three types of predators for over 500 prey generations. The predators either used: (1) no social information (NS), (2) SI only, or (3) PI. Surprisingly, the prey evolved the highest clumpiness for NS predators. Prey evolved towards smaller clump sizes with SI predators and the clumps were marginally larger when predators used PI. The result is due to the prey evolving the minimum clumpiness required to cause maximal ISI use by their predators. We discuss how this response by prey may favour the use of PI over SI in their ISI-using predators.

III.2 Introduction

A great deal of research has been invested in exploring how predators influence the distribution of their prey. Most studies have focused on solitary foragers, and the general pattern emerges that prey evolve towards clumped distributions, a response that reduces the efficiency of predator searching (Taylor 1977; Bonmarco et al. 2007). Yet, a large number of predators forage socially. Social foraging has been shown to impact predator efficiency at detecting prey (Giraldeau and Beauchamp 1999). This will likely affect the anti-predator strategies evolved by their prey (Barrette and Giraldeau 2006) and, in turn, how predators adapt their search strategies.

When animals forage socially, individuals can obtain prey by searching for food patches themselves (producer tactic), but they may also search for patches discovered by others (scrounger tactic). To use the scrounger tactic, the predator must rely on information provided inadvertently by a successful producer. This inadvertent social information (ISI) can be of two types (Danchin et al. 2004); it may provide social information (SI) simply indicating the location of the resource or it may provide public information (PI; Valone 1989; 2007) that indicates the quality of the resource based on the performance of the individual already engaged in exploiting it. PI is thought to be better than SI because it is used preferentially when it is equally costly to obtain as other types of ISI (Coolen et al. 2005).

The gains from using ISI are likely to be negatively frequency dependent, as is the case for all producer-scrounger (PS) games (Barnard and Sibly 1981; Giraldeau and Caraco 2000); each tactic does better relative to the other when it is rare (Mottley and Giraldeau 2000). Under most circumstances, we expect the coexistence of both tactics at a stable equilibrium frequency (Mottley and Giraldeau 2000) where payoffs to each tactic are equal. Because scrounging, and hence ISI use, is mutually incompatible with producing (Coolen et al. 2001), any increase in the stable equilibrium frequency of scrounging results in a decreased number of producers that are concurrently searching for prey, and thus, lower predator search efficiency (Coolen 2002). Therefore, prey may be expected to evolve characteristics that can induce high rates of scrounging in their predators to reduce predator search efficiency (e.g. prey crypticity; Barrette and Giraldeau 2006). Another such trait may be prey clumpiness, because larger prey clump sizes are predicted to increase the stable equilibrium frequency of scrounging (Vickery et al. 1991; Caraco and Giraldeau 1991) and have been demonstrated to reduce predator efficiency at finding patches (Coolen 2002).

The behavioural traits of prey and predators engaged simultaneously in a PS game have only been examined on very short temporal scales, usually by monitoring the immediate response of players to environmental variation. Coolen et al. (2007) made an important step towards rectifying this by showing that scrounging can regulate both predator and prey populations. However, the impacts of scrounging, and thus the rate and type of information use, have never been empirically examined in an evolutionary context. Furthermore, despite the importance of predator-prey interactions in bridging behaviour and population ecology, very few studies have examined simultaneously the evolution of predator and prey, with most studies focusing only on prey response to predation pressure (Abrams 2000; Lima 2002) or vice versa (Murdoch 1973; Readshaw 1973; Cosner et al. 1999).

Here, we simulate a population of predators engaged in exploiting prey and thus explore a system of reciprocal evolution that integrates the behaviour of predator and prey in response to each other. First, we determine whether the optimal response of a predator is to increase its use of ISI and scrounge more when its prey form larger clumps. Then, we use a genetic algorithm approach to investigate whether prey confronted with predators that use: (1) no social information (NS), (2) SI, and (3) PI evolve towards the formation of increasingly larger clump sizes.

III.3 Methods

Agents played a producer-scrounger foraging game on a 40 × 40 grid, with predator population size set to 10 and prey population size set to 1000. At each time step, predators played either producer or scrounger. If they played producer, they would search for a prey patch at their immediate location, with discovery being assured if prey were present. If no prey were found, predators would move one square in one of the eight cardinal/sub-cardinal directions and select their strategy again. If predators played scrounger, they would scan the grid for conspecifics exploiting a patch and move towards them to join the discovery if one was found. Predators moving to scrounge at a patch moved at twice the normal rate of movement while searching (i.e. two grid squares per turn; Beauchamp 2000). If no conspecifics exploiting a patch were found, agents would move randomly as above and select their strategy again. Predators exploiting a patch, whether as producer or scrounger, would consume one prey item per time step, and continue feeding until the prey were depleted or the simulation ended, whichever occurred first. Predators had neither a minimum required, nor maximum allowed, food intake level. A complete simulation run consisted of 500 iterations of the above cycle.

In the NS scenario, predators can only discover food patches by searching themselves (producer tactic), and the scenario is provided as a reference against which to compare the other two scenarios in which predators do use ISI. In the SI scenario, predators can locate food themselves (producer tactic), or use foraging conspecifics as a cue to the location of food patches (scrounger tactic), and their allocation to each tactic is determined by the relative payoff sum (RPS) learning rule (Harley 1981). The relative payoff sum is a mathematical decision rule with the following form:

$$S_i(t) = x \cdot S_i(t-1) + (1-x) \cdot r_i + P_i(t) \qquad \text{(III.1)}$$

where $S_i(t)$ is the value placed on behavioural alternative i at time t, x is the memory factor which determines how highly the past is valued by determining how much the value placed on the alternative in previous rounds is used in calculating the current value placed on the alternative $(x \cdot (S_i(t-1)))$; this might be viewed intuitively as the degree to which past rewards to a strategy affect how the organism currently values the behaviour), r_i is the residual (the cutoff below which the valuation of the alternative cannot go even if the alternative should stop paying off entirely), and $P_i(t)$ is the payoff to the alternative during the current round, calculated as the amount of food ingested during that round by using that alternative (consequently, the payoff to at least one alternative will be zero each round since only one alternative can be used in a single time step). The probability p_s of using the scrounger tactic was then calculated by matching:

$$p_s = \frac{S_s(t)}{S_s(t) + S_p(t)} \qquad \text{(III.2)}$$

The use of a decision rule to model the learning of behaviour follows that found in Beauchamp (2000).

Finally, in the PI scenario, predators can search for food themselves (producer tactic), or use foraging conspecifics as a cue to the location of food patches (scrounger tactic), however, in this case, scroungers were also able to calculate whether they could reach a target patch before the patch was exhausted. This calculation was performed once, when the target search was performed, and was not recalculated as the scrounger moved towards the patch.

At the beginning of the simulation, prey were aggregated according to their clump size, which had initial values ranging randomly from 1-50. The clumping algorithm clumped all prey with an identical clump size together into patches as large as the coefficient itself: as an example, if 45 prey had a clump size of 10, four clumps of 10 would be produced as well as one clump of 5. The initial locations of predators and prey clumps were selected randomly from a uniform distribution over the set of two dimensional grid coordinates.

III.3.1 Genetic algorithms

Genetic algorithms are heuristic algorithms used to solve optimization problems by mimicking the methods of natural selection (selection,mutation,recombination; see Goldberg 1989). In behavioural biology, genetic algorithms are increasingly used to solve complex models of behaviour (Sumida et al. 1990; Hamblin and Hurd 2007; Ruxton and Beauchamp 2008).

Two genetic algorithms running in parallel were used to allow predator and prey characteristics to evolve. The performance of predators was calculated as the sum of the prey eaten over the entire time course of the simulation, while the performance of prey was calculated as the number of iterations in which prey remained alive; thus, for prey a maximal performance value would be 500, equal to the number of iterations for the simulation. In each genetic algorithm, agents were ranked by their performance and a new population was constructed using roulette-wheel selection (in which the chance of being selected for reproduction or replacement is related to fitness; Goldberg 1989; Lee and Kim 2005) over the top 15% of the population (selected for reproduction) and the bottom 15% of the population (selected for replacement). Mutation and recombination were then applied, with a mutation rate of 0.01 per locus and a recombination probability of 0.5. The simulation component was restarted with the new population when selection and reproduction were completed for both predator and prey populations. This cycle continued for 500 generations of the genetic algorithm.

A three loci chromosome was used for the predators, with one locus for each residual (producer and scrounger) and the memory factor. Values for the residual loci were $\{r_i \in \mathbb{R} | r_i \geq 0\}$ where $\mathbb{R}$ is the set of real numbers, while values for the memory factor were $\{x \in \mathbb{R} | 0 \leq x \leq 1\}$. For prey, the chromosome consisted of a single locus with an integer value ≥ 0, which was the clumping coefficient. Initial values were randomized; residual values were constrained between 0-5 initially, but allowed to mutate above that, while clumping coefficients were constrained between 0-50 but allowed to mutate above 50. Mutation steps (the allowable range in which mutation can modify the value of a locus) for residuals were $\in [1.0, 1.0]$, for the memory factor were $\in [0.1, 0.1]$, and for the clumping coefficient were $\in [3, 3]$. The results showed no sensitivity to these values.

The code for the genetic algorithm is based on that used and validated previously by Hamblin and Hurd (2007), rewritten in Python (Lee and Kim 2005; Bassi 2007). The source code is available from the authors upon request.

III.3.2 Simulation types

Two simulation types were performed. In the first, the prey used a constant clump size throughout the simulation so that the predators could modify their level of scrounging to maximize their gains. In the first set of simulations, prey clump size was fixed for each run with prey clump sizes stepped from 1 to 50 in steps of five (except the initial step: 1, 5, 10, 15, etc.). In the second set of simulations, prey clump size was free to evolve in the face of predators. For both simulation types, 25 replicates of each parameter combination were run.

To determine whether the simulated evolutionary patterns were directional (i.e. demonstrably different from a random walk), we assessed the patterns for signatures of an auto-regressive (AR) process, a moving average (MA) process, or some mixture of the two (all models were implemented in R ver. 2.6.2). If an AR process (without differentiation) or MA process is apparent in a model, then the pattern cannot have been created from a random walk or drift. We chose this ARIMA (auto-regressive integrated moving average) procedure over estimating a trendline (e.g. with a linear model) to better understand and describe temporal patterns in the data; ARIMA estimates how preceding points influence each point in a temporal data series to infer underlying evolutionary processes (Box and Jenkins 1976). ARIMA models are specified in the form (p, d, q), where p is the number of AR parameters, d is the level of differentiation, and q is the number of MA parameters. An example pattern generated from a random process (with or without drift) could thus be represented as (0, 0, 0).

To fit our ARIMA models, the series first had to be stabilized by determining the level of differentiation required (i.e. the variance associated with time must be removed). In our case, all models of clumping behaviour showed a very slow decay, indicating that a first-order differentiation (a model of the form (p, 1, q)) was necessary to remove the trend to make the data stationary. No transformations were required for models of scrounging behaviour. As our second step, we then examined temporal autocorrelation in the fitted series to determine whether any AR and MA terms belonged in the model, how many terms were necessary, and the coefficients of each of those terms.

III.4 Results

The predators increased their use of the scrounger tactic in response to increased average prey clump size. The increase in scrounger frequency however, was non-linear, and reached an asymptote when ca. 60% of individuals scrounged for prey in clump sizes ≥ 15 (Fig. III.1). The number of prey surviving at the end of a foraging bout mirrored those for scrounging: as clumping increased, so did the number of prey surviving (ANOVA: $F_{10,264} = 96.143$, $p < 0.0001$). For prey survival, as for scrounging, no further increase in prey survival was seen above clumping coefficients of 15, with prey survival reaching an asymptote near 600 (Fig. III.1B).

Prey evolved towards increased clumpiness (from 25 starting value to ca 40) with NS predators (Fig. III.2A). The increase in prey clump size was non-linear, with an asymptote clump size of 40 reached after approximately 250 generations. The best-fit ARIMA model (0, 1, 2) contained two MA terms with small coefficients ($\theta = -0.16$ and -0.11), which reflect the time series data fluctuating around a slowly increasing mean. These low MA coefficients indicate low resilience in the clumping data, but the fact that there were two MA terms in the model indicates the series is non-random and suggests a tendency to inflect in the direction of the exogenous perturbation (i.e. presence of predators all playing producer and searching for themselves).

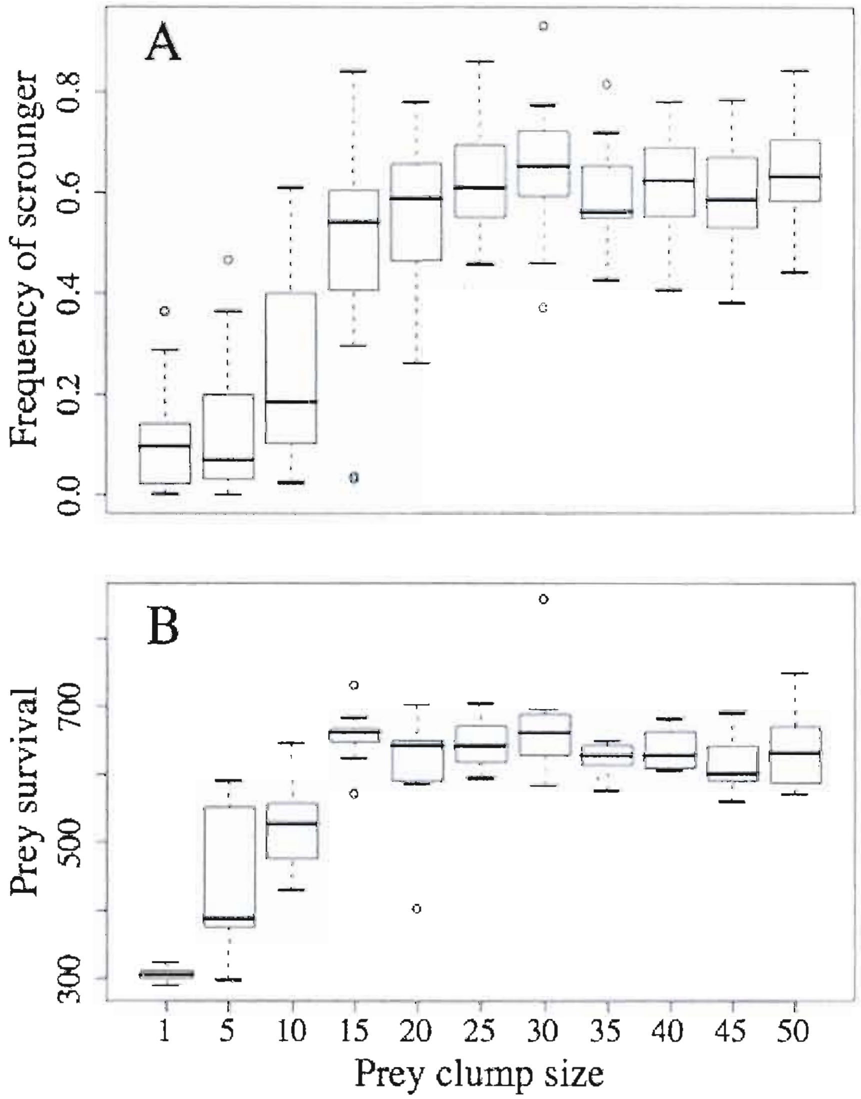

Figure III.1: The effect of prey clump size on a) the frequency of scrounger tactic use by predators, and b) prey survival (number of prey surviving from a starting population of 1000 prey). Prey clump size was held constant while predator behaviour was allowed to evolve under the social information scenario. Note that prey clump size refers to the clumping coefficients as described in the methods section.

When predators used SI and PI, the situation reversed. When predators used SI, prey evolved towards lower clump sizes (from 25 to ca. 15). The evolution of prey clump size was gradual, occurring throughout the 500 generations of the simulation. The best-fit ARIMA model (1, 1, 1) indicates the series was not the product of a random walk; the coefficient (θ) of the autocorrelation term was 0.51, and the coefficient (θ) of the MA term was 0.31. At the same time, predators decreased their use of the scrounger tactic from 0.5 to 0.4 (Fig. III.2B). The shift in predator behaviour was faster in the PI than in the SI situation, occurring within the first 75 generations, and remaining stable thereafter. Unlike clumping behaviour, temporal autocorrelation explains almost all variability in both scenarios involving scrounging behaviour (Fig. III.2B-C). In both cases, the best-fit ARIMA models (1, 1, 0) contained an AR term showing perfect autocorrelation ($\theta = 1.00$) and since the model contained a differentiation term, it is possible the series was generated from randomness.

When predators used PI, prey clump sizes decreased only slightly, from 25 to 20 and also appeared to stabilize more quickly compared with the NS situation, within 100 generations (Fig. III.2C). The best-fit ARIMA model (0, 1, 1) indicated the trend in clumping in this scenario was no different than might expected from a random-walk; the single MA term was very low ($\theta = 0.09$) and thus had little statistical power. At the same time, predators decreased their level of scrounging from 0.5 to 0.4, with the adjustment occurring here within the first 25 generations, and remaining relatively stable thereafter.

For all three scenarios, there was no change in prey survival rates over evolutionary time, but the survival rates of prey were better when predators used SI or PI compared with when they used NS (Fig. III.3); after controlling for a substantial random effect of 'run' (any of the 500 repeated measures of a population), a linear model shows a notably statistically significant difference between the three scenarios ($F_{2,1497} = 1254.3$, $p < 0.0001$). Tukey HSD post-hoc tests showed highly significant differences between all combinations of group means, showing that mean prey survival rates were higher in both the SI and PI than NS conditions and higher in the SI than in the PI condition.

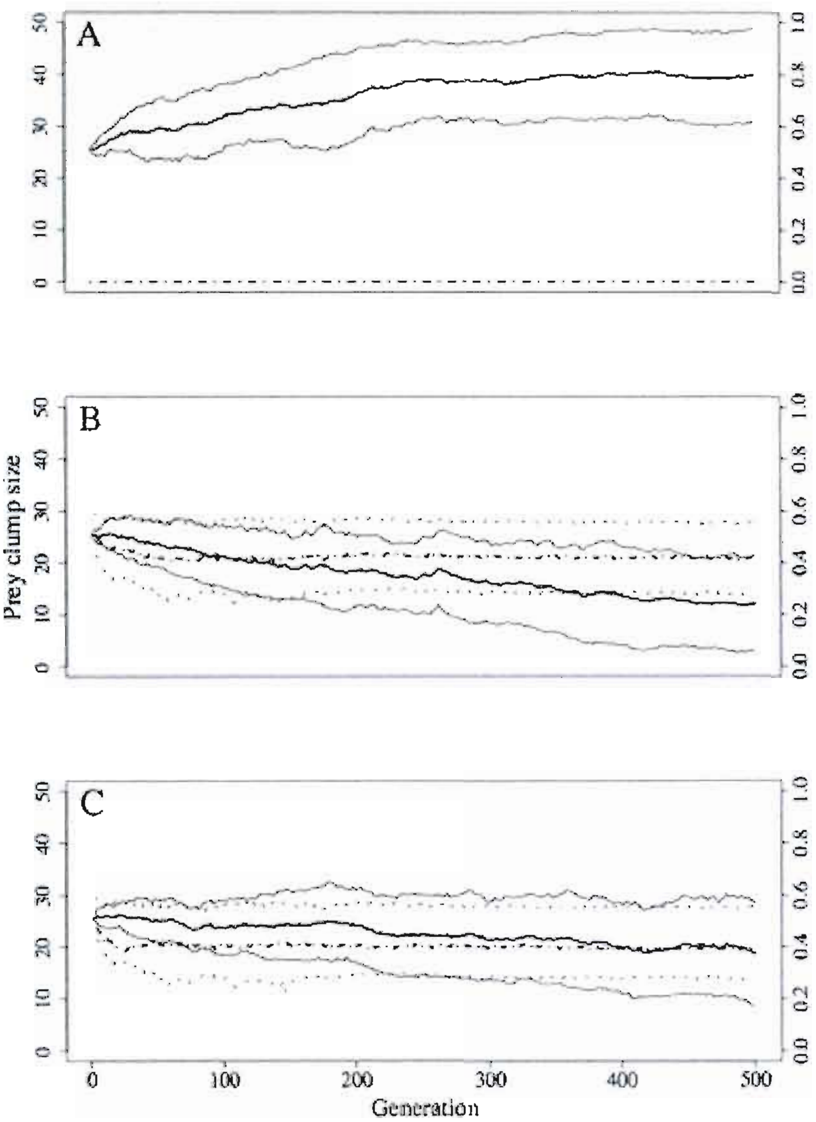

Figure III.2: The evolution of prey clump size (solid line) and the frequency of scrounger tactic use by predators (dotted line) when both traits are allowed to co-evolved under three scenarios of information use by the predators: a) no social information, b) social information, and c) public information. Note that prey clump size refers to the clumping coefficients as described in the methods section. Thick lines depict means, and thinner lines show ± 1 s.d.

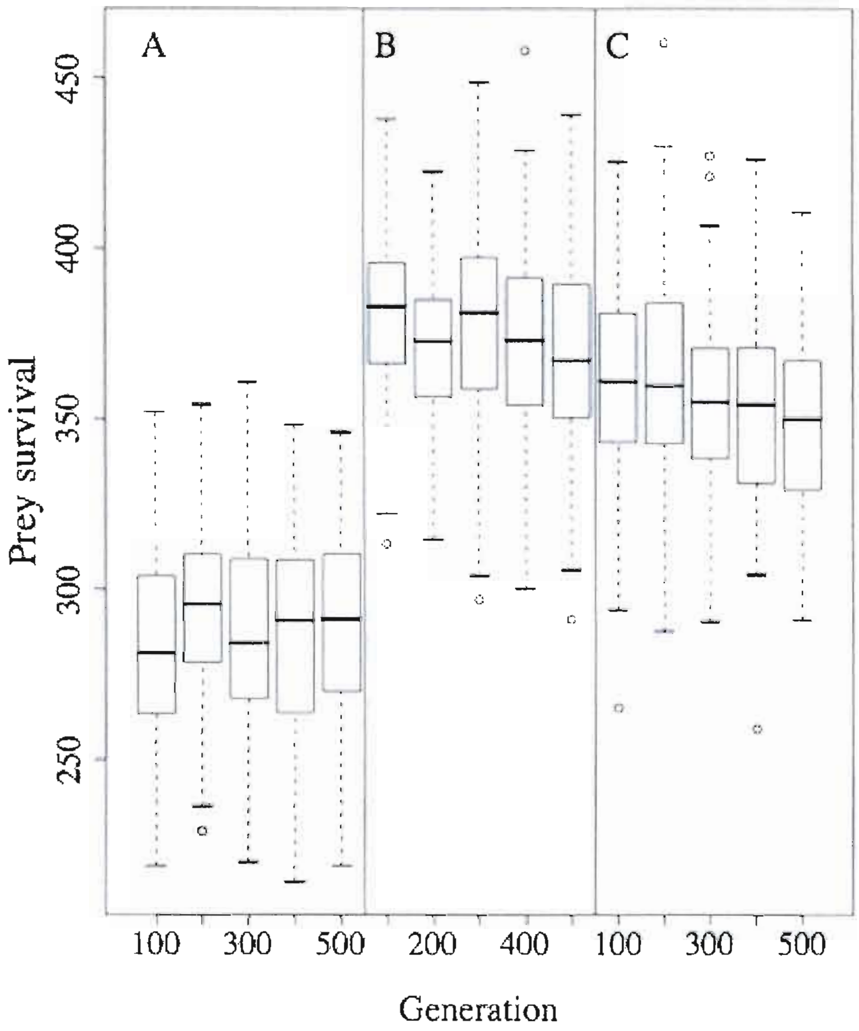

Figure III.3: Changes in prey survival rates across generations when predators use A) no social information, B) social information, and C) public information. Generations were pooled together as follows: 100 = generations 1 through 100, 200 = generations 101-200, 300 = generations 201-300, 400= generations 301-400, 500 = generations 401-500. The bold line of the box plots denote medians, while the higher and lower edge of the box denote the upper and lower quartiles respectively, the whiskers extend to the farther points that are still within 1.5 interquartile ranges from the quartiles.

III.5 Discussion

Our results show social information to be an important factor guiding the evolution of predator and prey characteristics; increased prey clump sizes induced increased levels of ISI use by predators (Fig. III.1A), which decreased predator search efficiency (as measured by prey survival; Fig. III.1B). This result is consistent with experimental tests of PS foraging games (Giraldeau and Caraco 2000; Coolen 2002). However, surprisingly, when prey were free to evolve, they did the opposite: they evolved towards the highest clumping against NS predators (Fig. III.2A) and smaller clump sizes against SI and PI predators (Fig. III.3B-C). This is the first demonstration of how information use by predators evolves in response to predator-prey dynamics, and here we explore this unanticipated result.

Both the rate-maximizing (Vickery et al. 1991) and risk-sensitive (Caraco and Giraldeau 1991; Barta and Giraldeau 2000) PS models predict an increase in scrounging frequency, and hence ISI use, with increasing prey clump size. However, the predicted effect of clump size on scrounging is non-linear; scrounging increases at a decreasing rate as clump size increases. As a result, any selective advantage of increased prey clumping will decrease as scrounging approaches asymptotic values. Our simulation of predators foraging for prey of different clump sizes supports this yet unrecognized non-linear effect. Our predators increased their use of scrounging when prey were in larger clumps but the level of scrounging reached an asymptote at around 60% scrounging, with no further increase in scrounging at clump sizes >15. Moreover, as expected, prey survival increased with increased scrounging (Giraldeau and Caraco 2000; Barrette and Giraldeau 2006).

We suggest that prey failing to evolve towards large clump sizes when faced with predators using ISI can be understood in light of these non-linear effects of clump size on scrounging frequency. When predators use SI, clump sizes decreased to around 15 prey items per patch. This number happens to match the minimum clump size found to induce the maximum level of scrounging in our predators (Fig. III.1A). Given that predators are already using ISI at its asymptotic frequency and will not evolve towards greater levels of ISI use, no further increase in clumping will benefit the prey in terms of reducing predator search efficiency. As a consequence, clump size ceases to evolve towards larger values. At this level of clumping, it is noteworthy that predators using only SI are induced to attempt to scrounge at all patches, even those that may well be exhausted by the time they reach them. This blindness to patch quality by the predators is still advantageous to the prey because it allows them to adapt to predator behaviour and clump only so much as to induce maximum levels of scrounging and impose an energetic cost on their predators. Such an advantage, however, may be reduced if the predators are better informed of patch quality and scrounging opportunities by the additional use of PI. When predators use PI, they do not join unless patch richness is such that they will have time to reach the patch before it is depleted.

Generally, information regarding resource location and quality that is more accurate and precise should increase predator efficiency (Valone 1996; King and Cowlishaw 2007). If we assume that NS predators have the least information, those that use SI have more and those using PI the most, then that was not the case in our study; prey survival was lowest against NS predators (Fig. III.3). The prey survived better when the predators used either SI or PI, which shows that scrounging, and hence ISI use of any form, actually reduced predator efficiency. Because scroungers inevitably exist in populations of social foragers (Giraldeau and Caraco 2000), such reduced predator efficiency will not be eliminated through selective pressure.

Predator efficiency tended to be higher when predators had access to PI compared with SI, as indicated by the lower prey survival rates (Fig. III.3). Given that the ability to use ISI evolves within predators, we would then expect selection to favour predators that shift from using SI to PI, which would allow them to forage more efficiently, mainly by avoiding scrounging attempts directed to less valuable food discoveries. As a result, predators may be less susceptible to manipulation by prey when they have access to PI. Consistent with this suggestion, predators reduced their investment in scrounging much more rapidly when they had access to PI compared with when they had access only to SI. This suggests there would be an advantage to prey to evolve traits that reduce the ability of predators to provide PI while they are being exploited. It would be interesting to explore what such traits would be like.

Our results illustrate some of the long-term consequences of predators opting to search for prey themselves or to collect SI/PI from others, which makes an important step towards understanding the effect of information use on evolution of predator and/or prey. However, we note that the results of our simulations require empirical testing; we have made several simplifying assumptions that might not hold in a realistic biological system. For example, we have assumed that predator survival was entirely determined by foraging success on a single prey species, and have kept population sizes constant throughout the simulated evolutionary process, thereby insulating our populations from density-dependent processes (see Abrams (2000) for a discussion on the impact of density-dependent process in predator-prey coevolution). Moreover, we have assumed that prey could not flee or adjust their behaviour to reduce their immediate risk of detection or mortality. Our conclusions may have been different if we assumed other benefits from clumping such as prey dilution and evasion, or improved predator detection. Nonetheless, we suggest that our genetic algorithm approach provides the possibility of addressing these intriguing possibilities.

III.6 Acknowledgements

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III.7 Bibliography

Abrams, P. A. (2000). The impact of habitat selection on the spatial heterogeneity of resources in varying environments. *Ecology*, 81:2902–2913.

Barnard, C. J. and Sibly, R. M. (1981). Producers and scroungers: A general model and its application to captive flocks of house sparrows. *Animal Behaviour*, 29:543–550.

Barrette, M. and Giraldeau, L.-A. (2006). Prey crypticity reduces the proportion of group members searching for food. *Animal Behaviour*, 71:1183–1189.

Barta, Z. and Giraldeau, L.-A. (2000). Daily patterns of optimal producer and scrounger use under predation hazard: A state-dependent dynamic game analysis. *The American Naturalist*, 155(4):570–582.

Bassi, S. (2007). A primer on python for life science researchers. *PLoS Computational Biology*, 3(11):2052–2057.

Beauchamp, G. (2000). Learning rules for social foragers: Implications for the producer-scrounger game and ideal free distribution theory. *Journal of Theoretical Biology*, 207:21–35.

Bonmarco, R., Firle, S. O., and Ekbom, B. (2007). Outbreak suppression by predators depends on spatial distribution of prey. *Ecological Modelling*, 201(2):163–170.

Box, G. E. P. and Jenkins, G. (1976). *Time Series Analysis: Forecasting and Control.* Holden-Day.

Caraco, T. and Giraldeau, L.-A. (1991). Social foraging: Producing and scrounging in a stochastic environment. *Journal of Theoretical Biology*, 153:559–583.

Coolen, I. (2002). Increasing foraging group size increases scrounger use and reduces searching efficiency in nutmeg mannikins (*Loncura punctulata*). *Behavioural Ecology and Sociobiology*, 52:232–238.

Coolen, I., Giraldeau, L.-A., and Lavoie, M. (2001). Head position as an indicator of producer and scrounger tactics in a ground-feeding bird. *Animal Behaviour*, 61:895–903.

Coolen, I., Giraldeau, L.-A., and Vickery, W. L. (2007). Scrounging behavior regulates population dynamics. *Oikos*, 116:533–539.

Coolen, I., Ward, A. J. W., Hart, P. J. B., and Laland, K. N. (2005). Foraging nine-spined sticklebacks prefer to rely on public information over simpler social cues. *Behavioral Ecology*, 16(5):856–870.

Cosner, C., Deangelis, D. L., Ault, J. S., and Olson, D. B. (1999). Effects of spatial grouping on the functional responses of predators. *Theoretical Population Biology*, 56:65–75.

Danchin, É., Giraldeau, L.-A., Valone, T. J., and Wagner, R. H. (2004). Public information: from nosy neighbors to cultural evolution. *Science*, 305:487–491.

Giraldeau, L.-A. and Beauchamp, G. (1999). Food exploitation: searching for the optimal joining policy. *Trends in Ecology & Evolution*, 14:102–106.

Giraldeau, L.-A. and Caraco, T. (2000). *Social Foraging Theory*. Monographs in Behavior and Ecology. Princeton University Press, New Jersey.

Goldberg, D. E. (1989). *Genetic algorithms in seach, optimization, and machine learning*. Addison-Wesley, Reading, Massachusetts.

Hamblin, S. and Hurd, P. L. (2007). Evolution's strategies: Genetic algorithms and game theory models. *Animal Behaviour*, 74(4):1005–1018.

Harley, C. B. (1981). Learning the evolutionarily stable strategy. *Journal of Theoretical Biology*, 89:611–633.

King, A. J. and Cowlishaw, G. (2007). When to use social information: the advantage of large group size in individual decision making. *Biology Letters*, 3:137–139.

Lee, W. and Kim, H.-Y. (2005). Genetic algorithm implementation in python. *Proceedings of the Fourth Annual ACIS International Conference on Computer and Information Science.*

Lima, S. L. (2002). Putting predators back into behavioral predator-prey interactions. *TRENDS in Ecology and Evolution*, 17(2):70–75.

Mottley, K. and Giraldeau, L.-A. (2000). Experimental evidence that group foragers can converge on predicted producer-scrounger equilibria. *Animal Behaviour,* 60:341–350.

Murdoch, M. W. (1973). Functional response of predators. *Journal of Applied Ecology,* 10:335–342.

Readshaw, J. L. (1973). Numerical response of predators to prey density. *Journal of Applied Ecology,* 10:342–351.

Ruxton, G. D. and Beauchamp, G. (2008). The application of genetic algorithms in behavioural ecology, illustrated with a model of anti-predator vigilance. *Journal of Theoretical Biology,* 250:435–448.

Sumida, B. H., Houston, A. I., McNamara, J. M., and Hamilton, W. D. (1990). Genetic algorithms and evolution. *Journal of Theoretical Biology,* 147:59–84.

Taylor, R. J. (1977). The value of clumping to prey. *Oecologia,* 30(3):285–294.

Valone, T. J. (1989). Group foraging, public information, and patch estimation. *Oikos,* 56(3):357–363.

Valone, T. J. (1996). Food-associated calls as public information about patch quality. *Oikos,* 77:153–157.

Valone, T. J. (2007). From eavesdropping on performance to copying the behavior of others: a review of public information use. *Behavioural Ecology and Sociobiology,* 62:1–14.

Vickery, W. L., Giraldeau, L.-A., Templeton, J. J., Kramer, D. L., and Chapman, C. A. (1991). Producers, scroungers, and group foraging. *The American Naturalist,* 137(6):847–863.

CHAPTER IV

SOCIAL FORAGING AND PERSONALITY

Preamble

This chapter is an article rejected for publication by *Behavioral Ecology*, now in revision for resubmission. All three authors developed the initial research question, and Ralf Kurvers and Luc-Alain Giraldeau provided input into the creation of the simulation model. Steven Hamblin programmed the simulation, did all simulation work, analyzed the data, produced the figures, and wrote the methods section. The paper was co-written by all three authors.

Scroungers are shy and producers are either: The co-evolution of boldness and alternative foraging tactics

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IV.1 Abstract

Animals foraging in groups may use either the producing or the scrounging tactic to obtain food items. Most models of producer - scrounger games generally assume that individuals are competitively equal such that pay-offs are independent of phenotype. However, personality, most notably boldness, is known to affect the use of foraging strategy. Here we use a genetic algorithm to determine how the use of producer and scrounger tactics interacts with the evolution of boldness, defined as the tendency to move away from conspecifics and explore the environment. Agents varied in boldness and scrounging probability and the genetic algorithm searched for the optimal combination of boldness and scrounging probability under different ecological parameters. Our simulations show that over a wide range of ecological conditions bold individuals evolve to play both producer and scrounger, whereas shy individuals remain confined to scrounging. An increase in patch density increased boldness, whereas patch richness did not affect boldness. We argue that this difference is due to the spatial dynamics: patch density, in contrast to patch richness, is a spatial component and therefore directly affects the optimal spatial positioning of individuals foraging in groups and as a result their boldness. Increased predation pressure resulted in the evolution of shyer individuals. For each parameter combination the genetic algorithm selected a single optimum level of boldness for all individuals demonstrating the absence of any negative frequency dependence of personality types in a producer - scrounger game. Our results show that differences in ecological conditions in a social foraging game may generate variation in boldness between populations.

IV.2 Introduction

Animals may either collect personal information about their environment, or they may observe other individuals to collect social information (Danchin et al. 2004). One of the best studied systems related to social information gathering is known as the producer - scrounger game (Barnard and Sibly 1981), in which individuals either search for food themselves (producing, = personal information) or make use of information about food made available by other group members (scrounging, = social information) (Hamblin et al. 2009). Most models of producer - scrounger games generally assume a symmetric game, a situation where phenotypic differences among individuals have no incidence on the payoffs they obtain from using one or the other foraging alternative. However, some phenotypic differences such as social dominance or competitive ability will likely affect the payoffs obtained via one or the other foraging alternative (Barta and Giraldeau 1998; Liker and Barta 2002; McCormack et al. 2007; King et al. 2009).

"Personality" in animal behaviour is used to describe differences between individuals in some behavioural and or physiological traits that remain consistent over time and context (Gosling and John 1999; Koolhaas et al. 1999; Carere and Eens 2005; Groothuis and Carere 2005). Different behavioural and physiological reactions have a genetic basis (van Oers et al. 2005) and are often correlated, suggesting that these differences are fundamental aspects of the behavioural organization of individuals. These animal personalities are documented at an increasingly quick pace (Réale et al. 2007; Biro and Stamps 2008; Sih and Bell 2008). More recently, experimental evidence shows that tactic choice in producer - scrounger games is related to personality differences; bolder barnacle geese (*Branta leucopsis*) use the producing tactic more often than shyer geese (Kurvers et al. 2010). This is in agreement with several studies which show that, in groups, bolder individuals approach food ('produce') more readily than shyer individuals (e.g. Beauchamp 2000; Dyer et al. 2009; Harcourt et al. 2009; Kurvers et al. 2009; Schuett and Dall 2009), whereas shyer individuals are more often observed following others (Dyer et al. 2009; Harcourt et al. 2009; Kurvers et al. 2009).

Although the association between bold producing and shy scrounging makes intuitive sense, there is no a priori reason to believe that it should be universal and applicable to all circumstances. For instance, could some foraging conditions call for dissociation between this personality trait and social foraging tactics? Do some foraging conditions call for monomorphic populations of intermediate boldness that allows for maximum flexibility in the use of producer and scrounger tactics? Here we incorporated personality differences in a producer - scrounger simulation model to explore the conditions under which personality and social foraging traits should coevolve. As a measure of the personality trait boldness, we varied the tendency of individuals to move away from other conspecifics and explore the environment. Bolder individuals were more likely to move away from other individuals than shyer individuals. We allowed individual agents to vary both in boldness as well as in scrounging probability in a spatially explicit producer-scrounger model. We used a genetic algorithm (Sumida et al. 1990) to find the optimal combination of boldness and foraging tactic while varying patch density, patch richness and predation pressure. Genetic algorithms mimic the action of natural selection to model population change over time (Hamblin and Hurd 2007; Ruxton and Beauchamp 2008), selecting the most successful individuals (i.e. those with the highest foraging rates) to reproduce in the next generation.

IV.3 The model

IV.3.1 The foraging simulation

Individuals searched for 200 time units for N_p patches containing N_s indivisible food items randomly distributed on a 500 by 500 grid. At each time unit individuals could either be feeding or not. When individuals were feeding they would continue feeding in that patch, consuming one food item per time unit until the patch depleted. When individuals were not feeding, their action consisted of two steps. In the first step, they chose whether or not to move towards other flock members and in the second step they searched for food opportunities. Choosing to move towards flock members was selected according to the probability P_m, the likelihood that an individual moves back to its conspecifics, calculated as:

$$P_m = e^{\beta \cdot b \cdot (1/d_m)} \tag{IV.1}$$

b is boldness (ranging from 0 to 1), β is a scaling parameter that affects the rate of moving back to conspecifics and dm is the median distance between the focal individual and its conspecifics. The probability of moving back to conspecifics increased with decreasing boldness score, implying that shyer individuals showed a higher tendency to move back to conspecifics as compared to bolder individuals. This is in agreement with the observation that shyer individuals show a lower tendency to split in smaller subgroups (Michelena et al. 2009) and have a higher shoaling tendency (Budaev 1997; Ward et al. 2004; Dyer et al. 2009). P_m increased with increasing median distance d_m, ensuring the maintenance of group cohesion.

If an individual decided to move towards the other flock members, its direction of movement was calculated as follows: a new direction was chosen by averaging the directions from the focal individual to each conspecific, weighted by the distance to each conspecific so that closer conspecifics weighted the new direction more heavily, according to the weighting function:

$$w(d_i) = W \cdot e^{(-d_i^2)/(2W^2)} \tag{IV.2}$$

where w is the calculated weight as a function of distance, W is a weighting constant and d_i is the Euclidean distance to a conspecific i. To handle edge cases where every conspecific was too far away to affect the direction of the focal individual, a new direction of movement would be calculated by adding a random component drawn from a Gaussian distribution that was added to the previous direction (a correlated random walk).

When searching for food an individual could either (1) search for food itself (producing) or (2) search for food discoveries of other individuals (scrounging). When producing, an individual investigated its close vicinity for food (as defined by a radius R_V), and if food was encountered, it started feeding in the next time unit. If no food was found, it took a step randomly. Random movement was calculated by selecting from a uniform distribution over the set of new directions within 45 degrees on either side of the current direction. When scrounging, an individual scanned the environment for producers exploiting a patch. The probability of detecting feeding producers p_f declined with distance d_i to the forager: $p_f = e^{-d_i/H^2}$. H determines the scrounging horizon; small values indicate that scroungers could only identify producers close by. If it identified a feeding producer it moved in its direction during the next time step with twice its normal step length. If the individual arrived in the next time step, it started feeding. If it did not arrive it continued in the direction of the foraging patch, provided that the patch still contained food items, until it reached the patch. If the patch was emptied during the movement, or if the scrounger did not find a forager in its initial search it moved randomly as described previously. A scrounger could only forage from the food discoveries of other foragers.

In all cases (moving to conspecifics or random movement), the length of the step S_I was a increasing function of boldness: $S_I = b * S_{\max}$. $S_{\max}$ is the maximal step length. To avoid a potential value of zero, a small random Gaussian component was added to every individual's step length. An increasing step length with increasing boldness reflects a higher exploration tendency for bold individuals, a well-described phenomenon since bold individuals are more often found in the leading edge of moving groups (Beauchamp 2000; Harcourt et al. 2009; Kurvers et al. 2009; Schuett and Dall 2009).

The predation probability P_P represents the chance that the furthest individuals from the flock will be predated each round (from 0 to 80%); each round a random uniform number was compared to the probability, and if it was lower, predation was applied to the population. To implement predation, the centroid (geometric center) of the population was first calculated as the average of each member's position. Each member of the population then received a distance score from the centroid, c_i and an individual was chosen to be predated proportionally to its distance score (with individual probability $p_i = c_i / \sum_j^N (c_j)$. This process was repeated each round until a maximum proportion of the population was preyed upon (the predation limit P_L, set to 5% of the population size) or the end of the simulation was reached.

IV.3.2 The genetic algorithm

An individual's strategy was encoded in a 2-locus real-valued chromosome, with locus 1 coding for the probability of scrounging and locus 2 coding for the value of boldness. Both loci ranged from 0 to 1, and all individuals in a given population size N_I started the genetic algorithm with a randomly generated chromosome value. At the end of each foraging simulation the number of consumed food items was computed for each individual and individuals were ranked on the basis of their fitness and the highest 60% was allowed to reproduce, all other individuals were removed from the population. Crossover probability was 0.9 implying that the probability of a selected chromosome to remain unchanged in the next generation (apart from any

Symbol	Meaning	Value or range
N_P	Number of patches	5,10,20,30,40,50,60
N_S	Number of individual food items in each patch	5,10,20,30,...,100
T	The length of the tournament	250
T_G	The number of generations for each run of the genetic algorithm	100
R_P	Spatial radius of a food patch	10
R_V	Radius of patch detection for producers	20
N_I	Population size	50
P_L	Predation limit	0.05
H	Scrounging horizon	10
β	Rate of moving back to conspecifics	25
W	Parameter of weighting function	50
P_P	Predation probability	0,0.2,0.4,0.6,0.8
S_{MAX}	Maximal step length	50
P_S	Scrounging probability	[0.0, 1.0]
b	Boldness	[0.0, 1.0]
P_F	Probability of detecting producers	[0.0, 1.0]
P_M	Probability of moving back to conspecifics	[0.0, 1.0]
S_I	Step length	[0.0, 1.0]

Table IV.1: Parameters of the simulation and behavioural variables.

changes due to mutation) is 0.1. The mutation rate was 0.1; if a locus was selected for mutation, it would be shifted from the old value by drawing a uniform random number between {-0.1, 0.1} and adding that to the old value. We varied patch density, patch richness and predation pressure (see Table IV.1 for parameter ranges).

IV.3.3 Measuring the evolution of personality and scrounging

For each parameter combination (see Table IV.1) we ran $T_G = 100$ generations (hereafter called a run) with five replicates per parameter combination for a total of 3850 runs. We analyzed the mean scrounging and boldness values, averaged over the last 10 generations of each run to reduce the effects of stochasticity.

For each run of the genetic algorithm, we searched for a polymorphism in scrounging and boldness using model-based cluster analysis on the final scrounging and boldness values for each member of the population using the Mclust package in R (Fraley and Raferty 2002; 2006); Mclust provides the optimal model according to the BIC (Bayesian Information Criterion) for expectation maximization in Gaussian mixture models. If a clear polymorphism of boldness and scrounging values was present (e.g., bold producers and shy scroungers), the cluster analysis would be expected to select a model with two clusters.

IV.4 Results

Boldness and scrounging became associated in the course of our runs: the shyest individuals ending up with high scrounging proportions, whereas the boldest individuals had low scrounging proportion (Fig. IV.1 and IV.2). High scrounging was observed over nearly the full range of boldness levels, except at the very extremes of boldness. Low scrounging was only observed at high values of boldness (Fig IV.1 and IV.2).

An increase in patch density led to an increase in boldness: under conditions of low patch density shy individuals were selected, but boldness increased rapidly with increasing patch density (Fig. IV.1). This pattern was consistent and appeared over the entire range of patch richness values (Fig. IV.1) and predation pressure, although the effect in the absence of predation was weaker (Fig. IV.2). An increase in patch density also led to a reduction in scrounging. This effect disappeared at high patch richness (Fig. IV.1). An increase in patch richness resulted in an increased scrounging, both for bold and shy individuals (Fig. IV.1). There was, however, no effect of patch richness on boldness (Fig. IV.1).

In the absence of predation, only bold individuals emerged (Fig. IV.2). When predation was present, shy individuals were selected and so boldness declined. There was no effect of predation on scrounging proportion (Fig. IV.2).

There was no evidence for a dichotomy in boldness. Model-based cluster analysis produced no evidence of preference for a model with 2 clusters (Table IV.2), and inspection of the data revealed that this was due to low variance in both scrounging and boldness across runs (mean $\sigma_{\mathrm{scr}} = 0.049$, mean $\sigma_{\mathrm{bold}} = 0.038$); the results of cluster analysis are bound to be unstable when overall variance is so restricted. Every run converged to a single value of boldness (max $\sigma_{\mathrm{bold}} = 0.067$), and only 54 runs

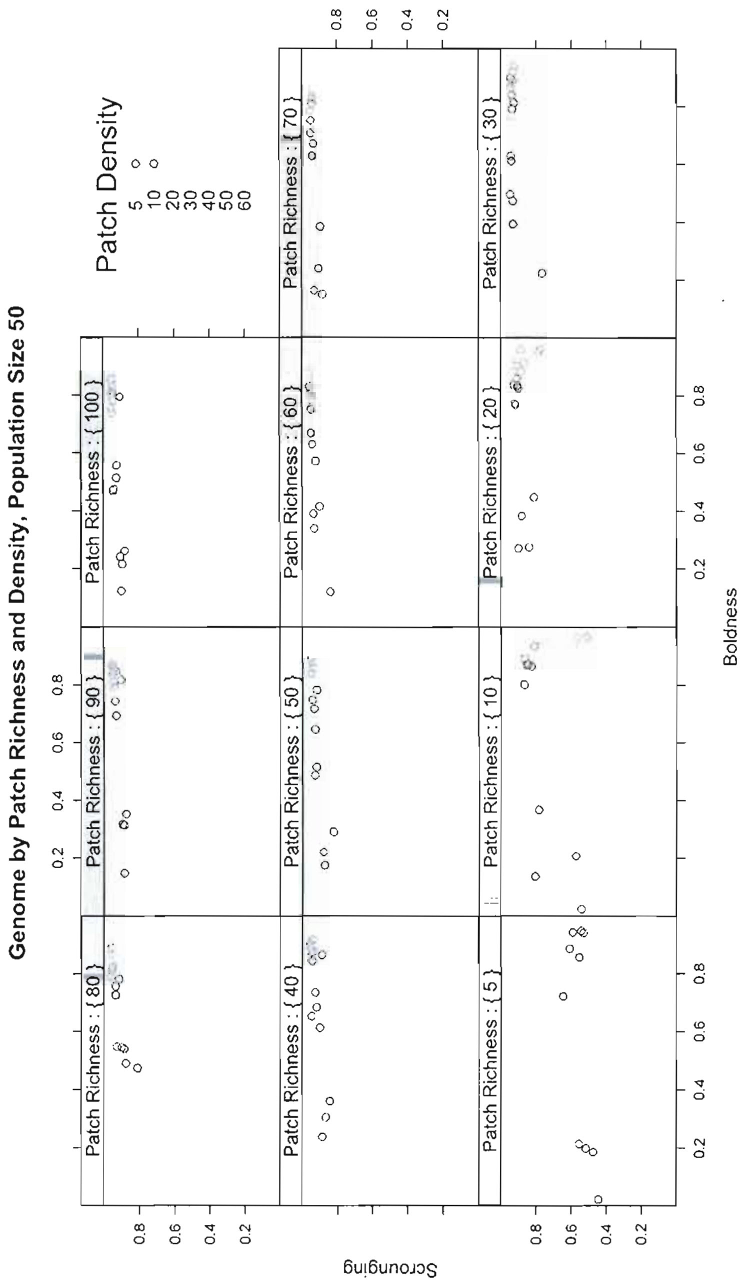

Figure IV.1: The effect of patch density and patch richness on boldness and scrounging values. An increase in patch density led to an increase in boldness and a reduction in scrounging, but the latter only under conditions of low / intermediate patch richness. An increase in patch richness resulted in increased scrounging, but there was no effect on boldness levels.

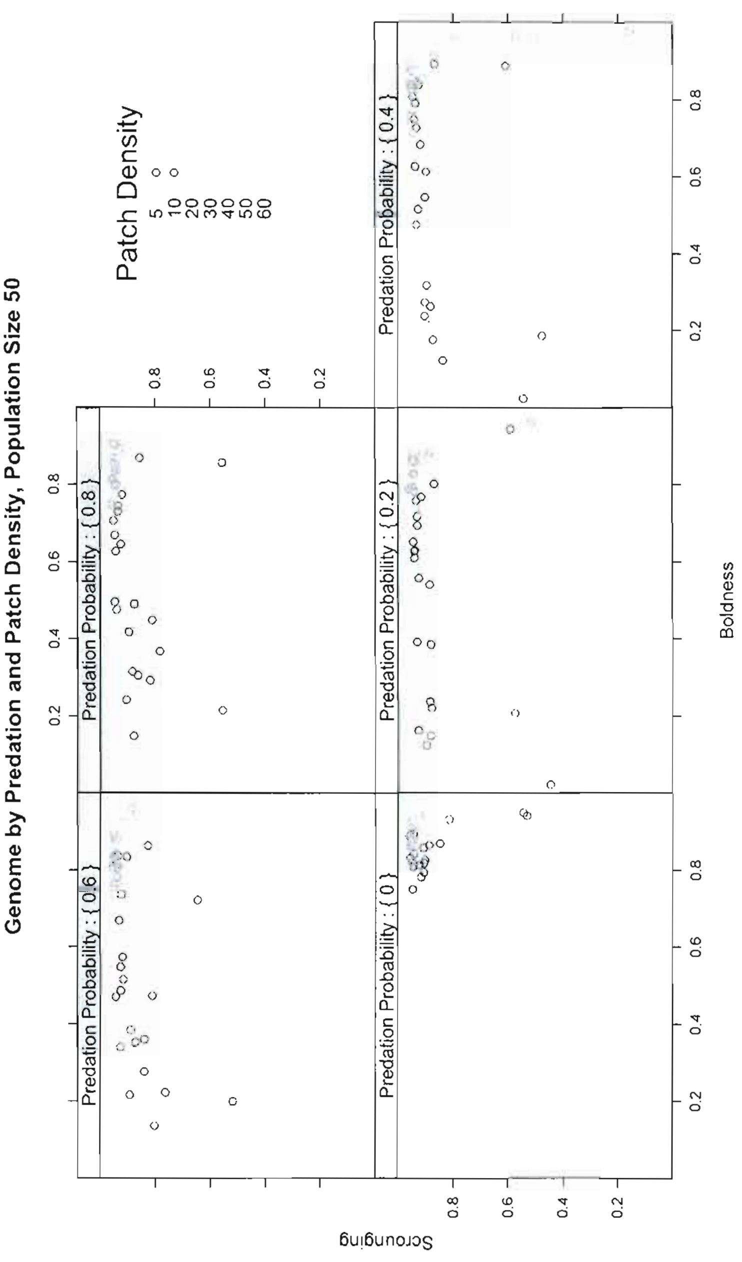

Figure IV.2: The effect of predation pressure and patch density on boldness and scrounging values. An increase in predation resulted in a reduction in boldness, but there was no effect on scrounging proportion.

Model components	1	2	3	4	5	6	7	8	9
Number of runs	116	394	507	534	548	448	509	398	396

Table IV.2: Optimal number of components selected in a cluster analysis of each run of the genetic algorithm.

failed to converge to a single value of scrounging ($\sigma_{\mathrm{scr}} > 0.1$) . Inspection of these runs confirmed the results of the statistical analysis in finding that no dimorphism in either boldness or scrounging existed.

IV.5 Discussion

The outcomes of our simulations showed a broad range of both boldness score as well as scrounging probability. Interestingly, high rates of scrounging were observed over nearly the full spectrum of boldness values, whereas high rates of producing were only observed at high boldness values. This conforms to earlier experimental evidence that shy barnacle geese scrounge more than bold individuals (Kurvers et al. 2010) and that boldness did not affect scrounging, but did affect producing, with bolder individuals producing a patch faster (Kurvers et al. 2011). At the same time these outcomes illustrate that the relationship between social foraging and boldness is not a simple linear relationship. Variation in patch density, patch richness and predation pressure all shaped the relationship between scrounging and boldness.

An increase in patch density led to a reduction in scrounging level, but only at low values of patch richness (see Fig. IV.1). This prediction conforms to Beauchamp (2008)'s results and is a consequence of the spatial explicitness of our model. The first models of producer - scrounger games (Barnard and Sibly 1981; Vickery et al. 1991; Caraco and Giraldeau 1991) assumed scroungers would instantaneously join food discoveries of other individuals and so obtain equal shares of any remaining food items independently of their initial spatial position. Under these conditions, scrounging frequency was independent of patch density. Beauchamp (2008) created a spatially explicit model of producers and scroungers, thereby introducing traveling time to scrounged food patches (hence a decrease in the share of food items scroungers received with increasing distance). Beauchamp and Giraldeau (1997) demonstrated the importance of traveling time by showing that producing nutmeg mannikins, *Lonchura punctulata,* were more likely to leave a patch as scroungers arrived when search time was short. Our results confirm Beauchamp (2008)'s prediction that increasing patch density should reduce scrounging, because scrounging becomes less profitable when it is easy to find food (Clark and Mangel 1984). Koops and Giraldeau (1996) however, showed that increasing patch density resulted in an increase in the proportional use of scrounging. This increase in scrounging was, however, marginal and the total foraging area was small. An experiment varying patch density on a larger spatial scale would be valuable for testing our predictions. That an increase in patch density led to a reduction in scrounging level only under conditions of low patch richness makes sense. Under conditions of high patch richness, the profitability of scrounging increases rapidly, making producing relatively less profitable. Interestingly, an increase in patch density not only led to a reduction in scrounging level, but also favored an increase in boldness. When patches are poor the bolder individuals turn to producing such that at a high density of poor patches more producing emerges. Producer success depends on the producers' ability to distance themselves from conspecifics (Barta et al. 1997; Flynn and Giraldeau 2001). In our simulation a tendency to increase one's distance from conspecifics is achieved by increasing boldness, meaning that shy individuals forage at close proximity of each other, whereas bolder individuals are more spaced out. We think that these spatial dynamics are the single most important reason for the various effects we found on boldness. At low patch density the tendency to scrounge increases and the success of scrounging requires remaining close to potential producers (Barta et al. 1997; Flynn and Giraldeau 2001). So, our simulations predict that shy individuals do best at low patch densities. Our simulation results also suggest that gregariousness, the tendency to remain close to each other, breaks down at high patch density, because selection favors bold producers (that is spaced out solitary foraging). Several models predict that group foraging is more likely to occur only when food patches are scarce and rich (Waltz 1982; Clark and Mangel 1986; Barta and Giraldeau 2001), exactly the situation where our simulation predicts the most scrounging and closest proximity (i.e., shyest individuals). Interestingly, in our simulation boldness declined with increasing patch scarcity when patches were rich, but scrounging levels remained similar. This suggests that although scrounging levels are similar, the optimal spatial positioning of individuals in a foraging group depends on the number of patches. Most likely, when there are very few patches finding a patch is a rare event such that one needs to remain close to as many other group mates as possible if scrounging is to be profitable at all. However, when there are many patches, finding a patch is commoner so scrounging success is less dependent on the number of individuals kept close by.

Increasing patch richness resulted in an increase in scrounging frequency. This was a very consistent pattern across the complete range of boldness values. This is in agreement with both empirical and theoretical results for producer - scrounger games (Giraldeau and Livoreil 1998; Coolen et al. 2001; Coolen 2002; Beauchamp 2008): with an increase in patch richness the finder's share decreases (or seen from a scrounger perspective: the joiner's share increases), resulting in an increase in scrounging pay-offs. Patch richness, in contrast to patch density, did not affect boldness. We think that this is due to the spatial dynamics of the producer - scrounger game: patch richness is not a spatial component, whereas patch density is primarily a spatial component. Because patch richness is not a spatial component it does not affect the optimal spatial positioning of individuals in a foraging flock and this is, we think, the reason for the lack of effect of patch richness on boldness. Interestingly, Michelena et al. (2009) showed that the spatial distribution of bold and shy Scottish blackface sheep, *Ovis aries*, differed with bold sheep splitting into subgroups at smaller group sizes than shy sheep. The differences in spatial distribution could be simulated by a model that included simple rules on sensitivity to crowding and social attraction (Michelena et al. 2010). Although our model is different as it runs over an evolutionary time scale both their and our models show the importance of differences in social attraction rules on the spatial dynamics of individuals foraging in groups. Clearly, how personality affects social attraction rules between group living individuals and how this in turns affects collective processes is an exciting avenue for further research.

Predation pressure did not affect scrounging probability. This is in line with Coolen and Giraldeau (2003) and Ha and Ha (2003) who show that predation danger did not affect the stable equilibrium frequency of scrounging (but see Barta et al. 2004). Although predation danger did not affect the stable equilibrium frequency of scrounging (group response), individual manipulation of predation danger (individual response) did affect scrounging: individual zebra finches, *Taeniopygia guttata*, increased their scrounging frequency when treated with wing-load manipulations that increased their vulnerability (Mathot and Giraldeau 2010). How predation risk shapes scrounging pay offs and frequency is highly affected by the (in)compatibility between scrounging tactic and anti predatory vigilance. If the scrounging tactic is compatible with anti predatory vigilance increased predation risk should lead to more scrounging. In our simulations, using the scrounging tactic and scanning for predators were not compatible, following Coolen and Giraldeau (2003) who show that scrounging tactic and anti predatory vigilance are not compatible in nutmeg manikins (but see Ranta et al. 1998; Mathot and Giraldeau 2010).

As predicted by Stamps (1991) we found that increasing the risk of predation resulted in reduced boldness and hence shyer individuals. In our model the risk of being preyed upon increased with increasing distance from the flock centre. Because bolder individuals moved further out of the centre of the group, they suffered an increased predation pressure. Differences in boldness are suggested at least in part to be the consequence of differences in predation pressure (Bell and Sih 2007). Cote et al. (2008) went as far as suggesting that the costs of being bold likely disappear in the absence of predation. In that case there is a trade-off between food intake rate and predation risk, with bold individuals enjoying a higher food intake rate but also a higher risk of being predated. A positive correlation between boldness and food intake rate has indeed been reported in several species (for review see Biro and Stamps 2008) and there is now also evidence accumulating that bolder individuals suffer a higher predation risk (Dugatkin 1992; Bremner-Harrison et al. 2004; Bell and Sih 2007; Carter et al. 2010), due to an increased tendency to expose themselves to risky situations. It is, however, noteworthy that boldness may also be favored by increased predation pressure, if bolder individuals engage more in predator inspection events and predator inspection deters predators as is suggested by a study in bighorn sheep ewes (Réale and Festa-Bianchet 2003).

Our simulations showed that differences in patch density and predation pressure result in a broad range of different optimal combinations of boldness and scrounging across runs. Differences in selection pressures (either in space or time) in a social foraging game may generate different optimal boldness levels, suggesting that spatio-temporal dynamics (i.e., fluctuating environments) may cause variation in boldness levels between populations (see also Dall et al. 2004; Dingemanse et al. 2004; 2009; Bell and Sih 2007; Smith and Blumstein 2008). Populations evolved towards a monomorphism where a single optimal level of boldness characterized all the individuals in the population. We found no evidence for a stable co-existence of different personality types within one population submitted to a given assortment of environmental conditions. Playing the producer - scrounger game seems thus to be insufficient to allow the evolution and maintenance of different personality types by means of, for example, negative frequency dependent selection as illustrated by recent theoretical work (Wolf et al. 2008; McNamara et al. 2009; Wolf and Weissing 2011).

To conclude, we have shown that boldness and social foraging are linked. Bold individuals are able to play both producer and scrounger, whereas shy individuals are confined to the scrounging tactic. In general an individual's scrounging probability increased with decreasing boldness. An increase in patch density resulted in the evolution of bolder individuals, whereas patch richness did not affect boldness levels. The genetic algorithm selected a single optimum level of boldness for each parameter combination, thereby showing no evidence for a negative frequency dependent selection of personality types in a producer - scrounger game.

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IV.7 Bibliography

Barnard, C. J. and Sibly, R. M. (1981). Producers and scroungers: A general model and its application to captive flocks of house sparrows. *Animal Behaviour*, 29:543–550.

Barta, Z., Flynn, R., and Giraldeau, L.-A. (1997). Geometry for a selfish foraging group: a genetic algorithm approach. *Proceedings of the Royal Society of London. Series B, Biological Sciences*, 264:1233–1238.

Barta, Z. and Giraldeau, L.-A. (1998). The effect of dominance hierarchy on the use of alternative foraging tactics: a phenotype-limited producing-scrounging game. *Behavioural Ecology and Sociobiology*, 42:217–223.

Barta, Z. and Giraldeau, L.-A. (2001). Breeding colonies as information centers: a reappraisal of information-based hypotheses using the producer-scrounger game. *Behavioural Ecology*, 12(2):121–127.

Barta, Z., Liker, A., and Mónus, F. (2004). The effects of predation risk on the use of social foraging tactics. *Animal Behaviour*, 67:301–308.

Beauchamp, G. (2000). Individual differences in activity and exploration influence leadership in pairs of foraging zebra finches. *Behaviour*, 137:301–314.

Beauchamp, G. (2008). A spatial model of producing and scrounging. *Animal Behaviour*, 76:1935–1942.

Beauchamp, G. and Giraldeau, L.-A. (1997). Patch exploitation in a producer-scrounger system: test of a hypothesis using flocks of spice finches (*Lonchura punctulata*). *Behavioural Ecology*, 8:54–59.

Bell, A. and Sih, A. (2007). Exposure to predation generates personality in three-spined sticklebacks *Gasterosteus aculeatus*. *Ecology Letters*, 10:828–834.

Biro, P. A. and Stamps, J. A. (2008). Are animal personality traits linked to life-history productivity? *Trends in Ecology & Evolution*, 23(7):361–368.

Bremner-Harrison, S., Prodohl, P. A., and Elwood, R. W. (2004). Behavioural trait assessment as a release criterion: boldness predicts early death in a reintroduction programme of captive-bred swift vox (*Vulpes velox*). *Animal Conservation*, 7:313–320.

Budaev, S. V. (1997). "personality" in the guppy (*Poecilia reticulata*): a correlational study of exploratory behavior and social tendency. *Journal of Comparative Psychology*, 111(4):399–411.

Caraco, T. and Giraldeau, L.-A. (1991). Social foraging: Producing and scrounging in a stochastic environment. *Journal of Theoretical Biology*, 153:559–583.

Carere, C. and Eens, M. (2005). Unravelling animal personalities: how and why individuals consistently differ. *Behaviour*, 142(9):1149–1157.

Carter, A. J., Goldizen, A. W., and Tromp, S. A. (2010). Agamas exhibit behavioral syndromes: bolder males bask and feed more but may suffer higher predation. *Behavioural Ecology*, 21(655-661).

Clark, C. W. and Mangel, M. (1984). Foraging and flocking strategies: Information in an uncertain environment. *The American Naturalist*, 123(5):626–641.

Clark, C. W. and Mangel, M. (1986). The evolutionary advantages of group foraging. *Theoretical Population Biology*, 30:45–75.

Coolen, I. (2002). Increasing foraging group size increases scrounger use and reduces searching efficiency in nutmeg mannikins (*Loncura punctulata*). *Behavioural Ecology and Sociobiology*, 52:232–238.

Coolen, I. and Giraldeau, L.-A. (2003). Incompatibility between antipredatory vigilance and scrounger tactic in nutmeg mannikins, *Lonchura punctulata*. *Animal Behaviour*, 66:657–664.

Coolen, I., Giraldeau, L.-A., and Lavoie, M. (2001). Head position as an indicator of producer and scrounger tactics in a ground-feeding bird. *Animal Behaviour*, 61:895–903.

Cote, J., Dreiss, A., and Clobert, J. (2008). Social personality trait and fitness. *Proceedings of the Royal Society of London. Series B, Biological Sciences*, 275(1653):2851–2858.

Dall, S. R. X., Houston, A. I., and McNamara, J. M. (2004). The behavioural ecology of personality: consistent individual differences from an adaptive perspective. *Ecology Letters*, 7:734–739.

Danchin, É., Giraldeau, L.-A., Valone, T. J., and Wagner, R. H. (2004). Public information: from nosy neighbors to cultural evolution. *Science*, 305:487–491.

Dingemanse, N. J., Both, C., Drent, P. J., and Tinbergen, J. M. (2004). Fitness consequences of avian personalities in a fluctuating environment. *Proceedings of the Royal Society of London. Series B, Biological Sciences*, 271:847–852.

Dingemanse, N. J., Kazem, A. J. N., Réale, D., and Wright, J. (2009). Behavioural reaction norms: animal personality meets individual plasticity. *TRENDS in Ecology and Evolution.*

Dugatkin, L. A. (1992). Tendency to inspect predators predicts mortality risk in the guppy (*Poecilia Reticulata*). *Behavioural Ecology*, 3:124–127.

Dyer, J. R. G., Croft, D. P., Morrell, L. J., and Krause, J. (2009). Shoal composition determines foraging success in the guppy. *Behavioral Ecology*, 20(1):165–171.

Flynn, R. and Giraldeau, L.-A. (2001). Producer-scrounger games in a spatially explicit world: Tactic use influences flock geometry of spice finches. *Ethology*, 107:249–257.

Fraley, C. and Raferty, A. E. (2002). Model-based clustering, discriminant analysis, and density estimation. *Journal of the American Statistical Association*, 97:611–631.

Fraley, C. and Raferty, A. E. (2006). MCLUST version 3 for R: Normal mixture modeling and model-based clustering. Technical report, Department of Statistics, University of Washington.

Giraldeau, L.-A. and Livoreil, B. (1998). Game theory and social foraging. In Dugatkin, L. A. and Reeve, H. K., editors, *Game theory and animal behaviour.*, pages 16–37. Oxford University Press, New York.

Gosling, S. D. and John, O. P. (1999). Personality dimensions in nonhuman animals: a cross-species review. *Current Directions in Psychological Science*, 8(3):69–75.

Groothuis, T. G. G. and Carere, C. (2005). Avian personalities: characterization and epigenesis. *Neuroscience and Biobehavioral Reviews*, 29(1):137–150.

Ha, R. R. and Ha, J. C. (2003). Effects of ecology and prey characteristics on the use of alternative social foraging tactics in crows, *Corvus caurinus. Animal Behavior*, 66:309–316.

Hamblin, S. and Hurd, P. L. (2007). Evolution's strategies: Genetic algorithms and game theory models. *Animal Behaviour*, 74(4):1005–1018.

Hamblin, S., Mathot, K. J., Morand-Ferron, J., Nocera, J. J., Rieucau, G., and Giraldeau, L.-A. (2009). Predator inadvertent social information use favours reduced clumping of its prey. *Oikos*, 119(2):286–291.

Harcourt, J. L., Ang, T. Z., Sweetman, G., Johnstone, R. A., and Manica, A. (2009). Social feedback and the emergence of leaders and followers. *Current Biology*, 19(3):248–252.

King, A. J., Isaac, N. J. B., and Cowlishaw, G. (2009). Ecological, social and reproductive factors shape producer-scrounger dynamics in baboons. *Behavioral Ecology*.

Koolhaas, J. M., Korte, S. M., de Boer, S. F., Vegt, B. J. V. D., Reenen, C. G. V., Hopster, H., Jong, I. C. D., Ruis, M. A. W., and Blokhuis, H. J. (1999). Coping styles in animals: current status in behavior and stress-physiology. *Neuroscience and Biobehavioral Reviews*, 23:925–935.

Koops, M. A. and Giraldeau, L.-A. (1996). Producer-scrounger foraging games in starlings: A test of rate-maximizing and risk-sensitive models. *Animal Behaviour*, 51:773–783.

Kurvers, R. H., Eijkelenkamp, B., van Oers, K., van Lith, B., van Wieren, S. E., Ydenberg, R. C., and Prins, H. H. (2009). Personality differences explain leadership in barnacle geese. *Animal Behaviour*, 78(2):447–453.

Kurvers, R. H., Nolet, B. A., Prins, H. H., Ydenberg, R. C., and van Oers, K. (2011). Boldness affects foraging decisions in barnacle geese: an experimental approach. submitted.

Kurvers, R. H., Prins, H. H., van Wieren, S. E., van Oers, K., Nolet, B. A., and Ydenberg, R. C. (2010). The effect of personality on social foraging: shy barnacle geese scrounge more. *Proceedings of the Royal Society of London. Series B, Biological Sciences*, 277(1681):601–608.

Liker, A. and Barta, Z. (2002). The effects of dominance on social foraging tactic use in house sparrows. *Behaviour*, 139(8):1061–1076.

Mathot, K. J. and Giraldeau, L.-A. (2010). Within-group relatedness can lead to higher levels of exploitation: a model and empirical test. *Behavioural Ecology*, 21(4):843–850.

McCormack, J. E., Jablonski, P. G., and Brown, J. L. (2007). Producer-scrounger roles and joining based on dominance in a free-living group of mexican jays (*Aphelocoma ultramarina*). *Behaviour*, 144(8):967–982.

McNamara, J. M., Stephens, P. A., Dall, S. R. X., and Houston, A. I. (2009). Evolution of trust and trustworthiness: social awareness favours personality differences. *Proceedings of the Royal Society of London. Series B, Biological Sciences*, 276:605–613.

Michelena, P., Jeanson, R., Deneubourg, J.-L., and Sibbald, A. M. (2010). Personality and collective decision-making in foraging herbivores. *Proceedings of the Royal Society of London. Series B, Biological Sciences*, 277(1684):1093–1099.

Michelena, P., Sibbald, A. M., Erhard, H. W., and McLeod, J. E. (2009). Effects of group size and personality on social foraging: the distribution of sheep across patches. *Behavioral Ecology*, 20(1):145–152.

Ranta, E., Peuhkuri, N., Hirvonen, H., and Barnard, C. J. (1998). Producers, scroungers, and the price of a free meal. *Animal Behaviour*, 55:737–744.

Réale, D. and Festa-Bianchet, M. (2003). Predator-induced natural selection on temperament in bighown ewes. *Animal Behaviour*, 65:463–470.

Réale, D., Reader, S. M., Sol, D., McDougall, P. T., and Dingemanse, N. J. (2007). Integrating animal temperament within ecology and evolution. *Biological Reviews*, 82(2):291–318.

Ruxton, G. D. and Beauchamp, G. (2008). The application of genetic algorithms in behavioural ecology, illustrated with a model of anti-predator vigilance. *Journal of Theoretical Biology*, 250:435–448.

Schuett, W. and Dall, S. R. X. (2009). Sex differences, social context and personality in zebra finches, *Taeniopygia guttata*. *Animal Behaviour*, 77:1041–1050.

Sih, A. and Bell, A. (2008). Insights for behavioral ecology from behavioral syndromes. *Advances in the Study of Behaviour*, 38:227–281.

Smith, B. R. and Blumstein, D. T. (2008). Fitness consequences of personality: a meta-analysis. *Behavioral Ecology*, 19:448–455.

Stamps, J. A. (1991). Why evolutionary issues are reviving interest in proximate behavioral mechanisms. *American Zoologist*, 31:338–348.

Sumida, B. H., Houston, A. I., McNamara, J. M., and Hamilton, W. D. (1990). Genetic algorithms and evolution. *Journal of Theoretical Biology*, 147:59–84.

van Oers, K., de Jonh, G., van Noordwijk, A. J., Kempenaers, B., and Drent, P. J. (2005). Contribution of genetics to the study of animal personalities: a review of case studies. *Behaviour*, 142:1185–1206.

Vickery, W. L., Giraldeau, L.-A., Templeton, J. J., Kramer, D. L., and Chapman, C. A. (1991). Producers, scroungers, and group foraging. *The American Naturalist*, 137(6):847–863.

Waltz, E. C. (1982). Resource characteristics and the evolution of information-centers. *American Naturalist*, 119:73–90.

Ward, A. J. W., Thomas, P., Hart, P. J. B., and Krause, J. (2004). Correlates of boldness in three-spined sticklebacks (*Gasterosteus aculeatus*). *Behavioural Ecology and Sociobiology*, 55:561–568.

Wolf, M., van Doorn, G. S., and Weissing, F. J. (2008). Evolutionary emergence of responsive and unresponsive personalities. *Proceedings of the National Academy of Sciences*, 105(41):15825–15830.

Wolf, M. and Weissing, F. J. (2011). An explanatory framework for adaptive personality differences. *Philosophical Transactions of the Royal Society, Biological Sciences*, 365:3959–3968.

CHAPTER V

SOCIAL LEARNING FOR SOCIAL FORAGING

Preamble

This chapter is an article, rejected for publication by *The American Naturalist* in 2011, now in revision for resubmission. Steven Hamblin was responsible for the research question, developing the model, and performing all simulation work and analysis, as well as writing the manuscript. Luc-Alain Giraldeau provided guidance throughout the project and helped revise the manuscript for publication.

A rule of thumb for social foraging in a spatially explicit world.

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V.1 Abstract

Social foraging models like the producer-scrounger game have brought great insight to the study of strategic decision making in foraging situations, but existing producer-scrounger models do not specify a mechanism by which animals learn the equilibrium behaviour over ecological time. In this paper we present a spatially-explicit producer-scrounger model that uses a simple social learning mechanism, a heuristic rule of thumb in which individuals adopt the tactic - producer or scrounger - that has received the highest payoff for the individuals in their neighbourhood. We explore the effect of two key variables: the division of the food in a patch, and the size of an individual's neighbourhood (their effective group size). The results of the model show chaotic outcomes which possess features that match well with observations of animals playing producer-scrounger games, and the model makes several new predictions for future empirical work.

V.2 Introduction

In the study of the evolution of animal foraging behaviour, it has been traditional to separate efforts into two bodies of related but separate theory: optimal foraging theory (Stephens and Krebs 1986), which studies the foraging decisions of animals that do not depend on the presence or absence of other foragers, and social foraging theory (Giraldeau and Caraco 2000), which models foraging behaviour when a forager's decisions are directly related to the decisions of other foragers (e.g. under conditions of frequency dependence). In social foraging, one of the best studied models used to describe and explain this behaviour has been the producer-scrounger game (Barnard and Sibly 1981; Vickery et al. 1991; Giraldeau and Caraco 2000). This game theoretical model depicts foraging individuals as producers, who invest effort in finding exploitable resources such as food patches ('producing') and scroungers, who parasitize the effort of producers by sharing in their discoveries ('scrounging'). In the producer-scrounger game, each tactic (producing and scrounging) has a higher fitness when it is rare, leading to negative frequency-dependent selection and a mixed evolutionarily stable strategy (ESS: Maynard Smith 1982; Vickery et al. 1991). The classical producer-scrounger models have been tested in both laboratory and wild populations in multiple species, and have shown success in predicting qualitative patterns of behaviour (e.g. Steele and Hockey 1995; Wu and Giraldeau 2005; Barrette and Giraldeau 2006; Coolen et al. 2007; Morand-Ferron et al. 2007; Mathot and Giraldeau 2008; King et al. 2009; Kurvers et al. 2010; Giraldeau and Dubois 2008), but issues remain that should be addressed if the study of social foraging is to advance.

In particular, while evolutionary game theory predicts that animals will use fixed strategies (in the sense of unchanging, not to be confused with pure strategies), individuals consistently show flexibility in tactic use that changes over time to approach the equilibrium value and often responds to local conditions (Mottley and Giraldeau 2000; Morand-Ferron and Giraldeau 2010). This strongly suggests that individuals require decision rules that can sample alternatives and invest in each tactic in some way to determine the strategy that will maximize their payoffs (McNamara and Houston 2009), and we have indeed seen animals do this (an explicit example can be found in Mottley and Giraldeau 2000). But what mechanisms underlie this ability? The original producer-scrounger games (Barnard and Sibly 1981; Vickery et al. 1991; Giraldeau and Caraco 2000) suggest no mechanism beyond the genetic model assumed in ESS theory (Maynard Smith 1982). One line of research has sought to model the behavioural mechanisms responsible for this as 'learning rules', mathematical rules that describe how animals assign values to behavioural alternatives based on current and past information about their payoffs obtained by sampling; after an initial interest in learning rules waned (Harley 1981; Houston 1983; Selten and Hammerstein 1984; Milinski 1984; Houston and Sumida 1987; Harley 1987), researchers have begun to study them in greater detail again (Tracy and Seaman Jr. 1995; Beauchamp 2001; Hamblin and Giraldeau 2009; McNamara and Houston 2009).

To date, however, published work on learning rules has focused exclusively on the use of personal information obtained by sampling (i.e. payoffs that an individual obtains from their own use of producing or scrounging), and to our knowledge no models have used learning rules that incorporate social information. This omission is curious because many social animals are capable of some kind of social learning (Galef and Giraldeau 2001; Danchin et al. 2004), and is even more curious when learning rules have been applied to social foraging because the Producer Scrounger game is a game of social information use (Dall et al. 2005), in that individuals use social information about the foraging success of conspecifics to calculate their own optimal strategy.

In this study we present a model of social foraging in which individuals use a simple learning rule (a 'rule of thumb') based on social information use; the rule compares information about payoffs achieved by immediate neighbours (social information) to the payoff achieved by an individual (personal information; Dall et al. 2005) to make a decision about whether to produce or scrounge in the next time step. This rule is one of the simplest examples of social learning, and the use of similarly simple social learning rules has proven fruitful in the study of individual foraging (e.g. the Social Learning Strategies Tournament reviewed in Rendell et al. 2010). Our model assumes that social information is gathered by each individual from only its nearest neighbours and that foraging interactions occur only in this same neighbourhood (i.e. they are *local*); we interpret the resulting subset of the population that each individual interacts with as *effective group size.* This imparts spatial structure to the model which is important when group sizes increase beyond the small flocks typically studied under laboratory conditions. Indeed, we contend that in most real producer-scrounger systems, space will pose a real limitation to interactions which must be accounted for. For instance, in turbid waters fish may only be able to keep track of their immediate neighbours, while in ground-feeding birds vegetation may have the same effect (or detected food discoveries might be too far to be worth scrounging). It seems that in many group foraging scenarios, foragers may be limited to interacting with close neighbours.

A good way to model a producer-scrounger game with these characteristics is a cellular automaton (Wolfram 1984), a discrete-time model where space is represented by cells (foragers) on a grid with each cell in one of a finite set of states. All interactions are not only local but *regular*, occurring in a lattice formation; interactions are local in that each cell interacts with its immediate neighbours according to an *update rule* that specifies which state each cell will be in after the current time step has been completed. By adopting this model, we follow work on other evolutionary games such as the Prisoner's Dilemma (Nowak and May 1992; Nowak 2006). In doing so, we can compare our results to the predictions of the classical producer-scrounger model to describe changes to predictions resulting from incorporating social learning and spatial relationships, and we hope to derive a model which is deterministic, contains fewer assumptions and parameters than the individual-based models which have been used for these questions (Barta et al. 1997; Beauchamp 2000; Hamblin and Giraldeau 2009), and is easier to manipulate in future work.

With the model in hand, we ask questions related to the issues we have identified above. What are the consequences of using a social learning heuristic in a spatially-explicit social foraging task (the producer-scrounger game)? Exploring the properties of the model, we investigate whether individuals achieve a behavioural equilibrium (a stable equilibrium frequency, or SEF; Mottley and Giraldeau 2000; Giraldeau and Dubois 2008) and how the results compare to the predictions of the classical producer-scrounger model. Further, identifying an equilibrium is not the same as showing that the equilibrium is attainable (Nowak 1990; Hamblin and Hurd 2007), and so we investigate the conditions under which scroungers can invade a population of producers in this model. In our results and discussion, we focus on the effective group size as an important mediating variable in this model. We conclude by discussing the implications of our model for future empirical and theoretical study of the producer-scrounger game and social foraging in general.

V.3 Methods

Our cellular automaton model is a two dimensional grid of cells with a toroidal geometry (so that the cells on the left edge interact with those on the right edge, the top with the bottom, and opposite corners). Each cell is then assigned a tactic from the set {Producer, Scrounger}. Time proceeds in discrete units, and at each time step every cell on the grid simultaneously calculates its payoff and after that each compares its payoff to the other cells in its neighbourhood; if any of the neighbouring cells has a higher payoff, the focal cell adopts the tactic of the cell with the highest payoff for the next time step. Ties are broken randomly. After all cells have updated, the time step is over and the next time step begins.

V.3.1 Neighbourhoods

For our model, we define the local neighbourhood (area) for a focal cell to be a Moore neighbourhood of radius r (see Fig. V.1). The area for a given radius is $A_r = (2r+1)^2$. Cells interact with every other cell in their neighbourhood at each time step, and the radius is kept constant through each run of the automaton. In the discussion of our results, we interpret the set of individuals in the neighbourhood defined by a particular radius to be the *effective group size* for that radius; thus, a radius of 1 is an effective group size of 8. We use radii from 1 to 6 in this study, leading to effective group sizes of $\{8, 24, 48, 80, 120, 168\}$. We denote effective group size by G_E, and connect radius with effective group size by the notation $G_E(r) = n$, where r is the radius and n is the group size; thus $G_E(1) = 8$, $G_E(2) = 24$, and so on.

V.3.2 Payoffs

To calculate payoffs, each cell plays a 2-player game against each of its neighbours, one after the other, with results defined by Table V.1. Each cell has an inexhaustible food source which is accessible in discrete units worth one food unit per interaction. For simplicity, food units are treated as divisible; to model indivisible food units with the same payoff structure would simply require multiplying by a constant (which would maintain the rank-ordering of payoffs). The defining feature of this payoff matrix is the parameter α, which is a generalized form of the finder's share from the standard producer-scrounger model, and defines the amount that producers lose by

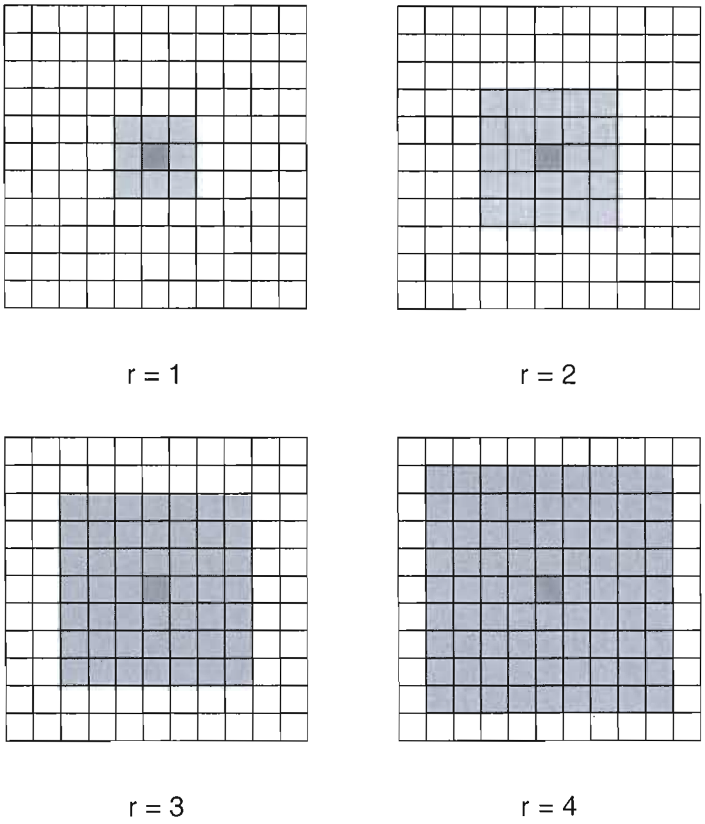

Figure V.1: Effective group size. The number of neighbours that each focal forager (red square) interacts with (grey squares) - the effective group size, G_E - is plotted as a function of the radius.

interacting with a scrounger; changes in α are functionally equivalent to changing the finder's share in standard producer-scrounger models.

To be clear, we provide an example. A focal forager has adopted the producer tactic for this time unit, and so produces one unit of food per interaction (play of the game) with each of its neighbours, for a maximum of 8 food units at $G_E(1)$, 24 at $G_E(2)$, and so on. For the purposes of this example, assume $G_E(1)$, and further assume that the focal agent's neighbours consist of a mix of 4 producers and 4 scroungers. Each play against a producer nets the focal producer half of the resource (top left cell in Table V.1), so they achieve a payoff of 0.5 against a fellow producer. Each play against a scrounger nets the focal producer a payoff equal to $1 - \alpha$, where α is the amount that the scrounger reduces the payoff of the producer by consuming that portion of the resource. The scrounger in such an interaction gets a payoff of α. Two scroungers playing against each other will score 0, because no-one has produced any food items.

	Producer	Scrounger
Producer	0.5	1 - α
Scrounger	α	0

Table V.1: Payoffs for the producer-scrounger game used as the basis for this model. See the text for an explanation of the significance of each payoff.

This payoff matrix has the form of the well-known game of Chicken (Rapoport and Guyer 1966), also known more famously as Hawk-Dove (Maynard Smith 1982), with a mixed equilibrium for any value of $\alpha > 0.50$. Though this has not been noted elsewhere to our knowledge, the standard producer-scrounger game model (Vickery et al. 1991; Giraldeau and Caraco 2000) follows the logic of an n-person continuous Chicken (Hawk-Dove). In our model, individual interactions are 2-player but the payoffs are still n-player because an individual's payoff in each round is a function of the number of scroungers in their neighbourhood; as the number of scroungers increases, payoffs to the scrounger tactic decrease just as in standard producer-scrounger models (Giraldeau and Caraco 2000, also see Arbilly et al. (2010) for a similar 2-player producer-scrounger game).

V.3.3 Updating

Figure V.2 shows the process for updating a focal cell (in this case, the centre-most cell). Each cell plays the game against its neighbours and receives a payoff. After the payoffs have been calculated for each cell, the cells simultaneously compare their payoffs to their neighbours; if any neighbour has a payoff which is higher than its own, the cell adopts the tactic of the neighbour with the highest payoff. The choice is recorded, and the tactic replacement is done before the next round begins but after all of the choices have been made (to avoid conflicts).

The updating rule used in our CA is a deterministic one, so knowing the initial configuration of the grid and the simulation parameters, it is possible to faithfully recreate any simulation run from beginning to end (though it is not necessarily possible to *predict* the outcome of a simulation; see Results). There are other possible updating rules, including stochastic rules that allow for a more realistic (but no longer replicable) updating, and which may have an effect on the results (e.g. Moyano and Sánchez 2009), but we do not deal with these here.

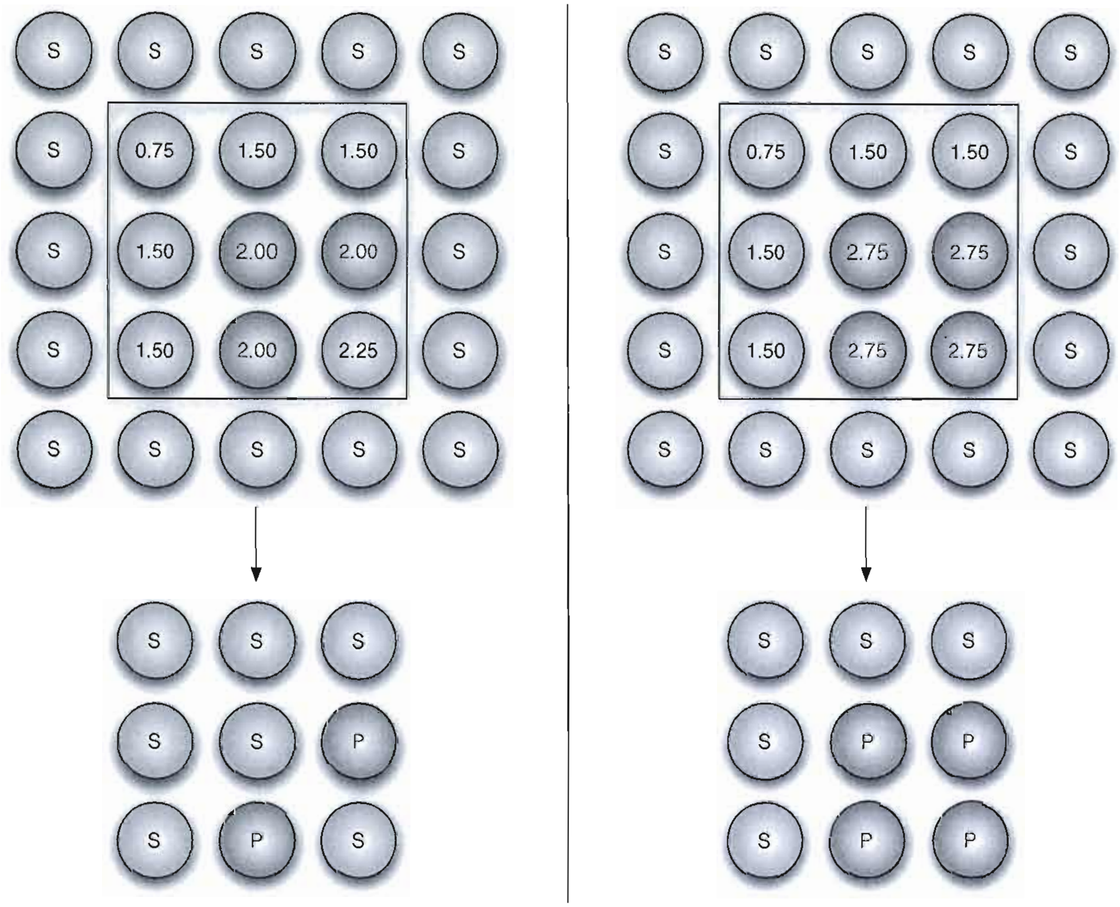

Figure V.2: Updating a cell. Red is scrounger and blue is producer. Cells calculate their payoffs against each of their neighbours, in this case using $G_E(1)$ and an α of 0.75. Here, we look at the cell in the centre of the grid section pictured. On the left hand side, the scrounger in the bottom-right of the focal cell's neighbourhood has a higher payoff than the focal cell, so the focal cell will become a scrounger in the next time step (though this is not depicted, so will the other two producers). On the right hand side, the addition of one more producer in the neighbourhood drives the focal cell's fitness high enough that it will no longer change to scrounger in the next time step.

V.3.4 Simulations

We did both individual and batch runs of the cellular automaton. For individual runs, we varied α and effective group sizes and inspected the results visually to classify outcomes and search for patterns. Individual runs could be started from an initial condition of random tactic choice in each cell, or the initial configuration could be specified down to the choice for each cell; this was used so that a single cell could be set to scrounger to see if it would invade a field of producers, or to see how many scroungers were stable for a given effective group size by setting the field to all-producer and then introducing one or more scroungers in a clump. We also did batch runs to collect data on scrounging and producing frequency as a function of the α and G_E values. In all cases, we used $G_E(r)$ with values of $r \in \{1,2,3,4,5,6\}$ (higher values were computationally prohibitive, since updating each cell requires playing against, and comparing payoffs to, an increasingly larger proportion of the grid) and α from 0.51 to 0.99. Simulations were run for 200 generations to allow enough time for a steady state to emerge, if one were forthcoming. Grid size was scaled by multiplying the side length of the grid by the radius, starting with a side length of 10 so that the grid sizes would be { 10x10, 20x20, 30x30, 40x40, 50x50, 60x60 }. This choice was made to scale the percentage of the grid area occupied by one cell's neighbourhood so that the percentage was roughly constant (if the area of the cell's neighbourhood for a given radius A_r is $A_r = 2(r+1)^2$, $\lim_{r\to\infty} A_r/(10r)^2 = 0.02$ and the percentage of the grid area occupied by one cell's neighbourhood asymptotes to 2% as the radius increases).

We also performed batch runs in which the initial population contained randomly selected producers and scroungers with each tactic having a 50% chance of being chosen in individual cells. 100 repetitions of each combination of α and G_E were performed, for a total of 29400 individual simulations. For batch runs, we report data on the mean frequency of scrounger played across the grid (of course, mean frequency of producer would be 1−frequency of scrounger), defined as the average of the proportion of the population playing scrounger at each generation over the total number of generations, and the variance of scrounger frequency.

We also report mean payoff to each tactic over the last 10 generations of each run to determine if a population equilibrium was reached; an average of 10 generations was used to smooth out the effects of oscillations with a short-period. To clarify the results, outcomes with producer proportions of 100% and 0%, representing the breakdown of social foraging, were omitted from the results and the difference in mean fitness values was normalized by the maximum scrounger fitness for the relevant value of α:

$$d_n = \frac{d_i}{G_E(r) \cdot \alpha} \tag{V.1}$$

where d_i is the raw mean difference in payoff to producer and scrounger, d_n is the normalized difference, and $G_E(r) \cdot \alpha$ is the maximum payoff achievable by an individual for a given value of α and effective group size. This normalization was used to eliminate the scaling of payoffs due to large values of G_E, and results in values of d_n between -1 and 1.

The source code for our simulation is written in Python (Bassi 2007), and is freely available from the authors upon request.

V.3.5 Comparison to predictions of deterministic rate-maximizing model

In the results, we compare the results of our simulation to the analytical predictions of the deterministic rate-maximizing (DRM) producer-scrounger model (put forth in Vickery et al. (1991), and discussed thoroughly in Giraldeau and Caraco (2000)). The DRM model result specifies that the predicted proportion of producing in a population, $\hat{p}$, is given by

$$\hat{p} = \frac{a}{F} + \frac{1}{G} \tag{V.2}$$

where a is the producer's advantage (the amount of a discovered patch's food that is available exclusively to the producer), F is the total amount of food in each patch, and G is the total group size. The anticipated number of producers and scroungers (1-$\hat{p}$) can than be calculated by multiplying $\hat{p}$ by the group size.

To compare results from our model to the predictions of the DRM model, we take α to be the proportion of the patch which is lost to scroungers and set $\alpha = 1 - (a/F)$. Group size G is the number of foragers on the grid ($G_E < G$), allowing us to compare $\hat{p}$ to the observed proportion of scrounging for any run of the simulation.

V.4 Results

V.4.1 Equilibrium outcomes

Do foraging agents in this model reach an equilibrium mixture of producing and scrounging behaviours as in the classical producer-scrounger models? At an equilibrium value the payoff to producer and scrounger should be equal (Maynard Smith 1982; Giraldeau and Caraco 2000); because this is a discrete model, we can consider an equilibrium to have been reached if the difference in payoffs is close to 0. Figure V.3 shows the normalized difference in mean payoff values to the producer and scrounger tactics for each value of α and G_E. Positive differences mean that producers did better than scroungers, while negative differences mean the reverse. The figure shows that payoff differences fluctuate around 0, signifying that approximate equilibrium values were achieved. The variance in payoff differences increases at intermediate values of α and as the effective group size increases, the range of values of α which show variation in payoffs decreases.

To determine what the equilibrium values in this model are, and to compare their results to the classical producer-scrounger model (the deterministic rate maximizing, or DRM, model), we plotted the mean scrounging values when starting from a random configuration of producers and scroungers in Figure V.4, with the predictions of the DRM model overlaid as the dashed line. The DRM model predictions are the same for all values of G_E because the radius (hence the effective group size) in the DRM model is effectively infinite, as scroungers can join producers anywhere with no cost.

Figure V.4 shows that the effect of α is decidedly non-linear, with the DRM model alternatively over- and under-predicting the amount of scrounging that will occur. As can be seen from the figure, the effective group size interacts strongly with α to define the region of α values that will lead to a mixed producer-scrounger equilibrium; this effect will be discussed further in section V.4.4. Note that at higher values of α, outcomes with 100% scrounging appear. This does not mean that the model predicts a population composed entirely of scroungers, which would be a biological impossibility; the model is instead predicting that a pathological outcome (extinction) will occur at these levels of α. In real populations, this would most likely lead to the collapse of social foraging. Similarly, outcomes with a mean scrounging of 0%

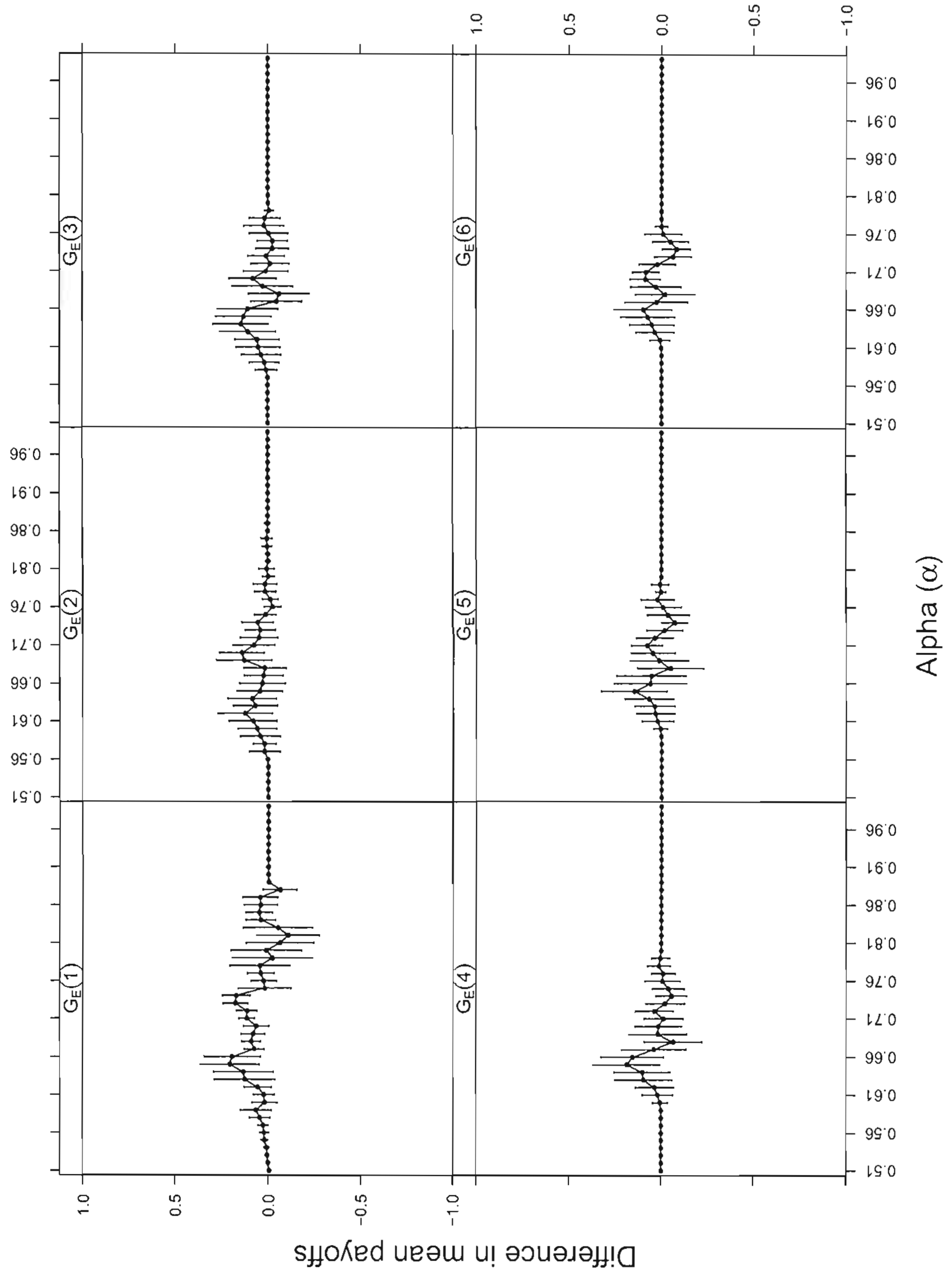

Figure V.3: Mean ± 1 S.D. of the normalized mean difference in payoffs for the last 10 generations of each run, as a function of the value of α and G_E. Normalization was done as discussed in the methods, and the difference is calculated by subtracting the payoff to scrounger from the payoff to producer; thus, positive differences mean that producers performed better and negative differences mean that producers performed worse.

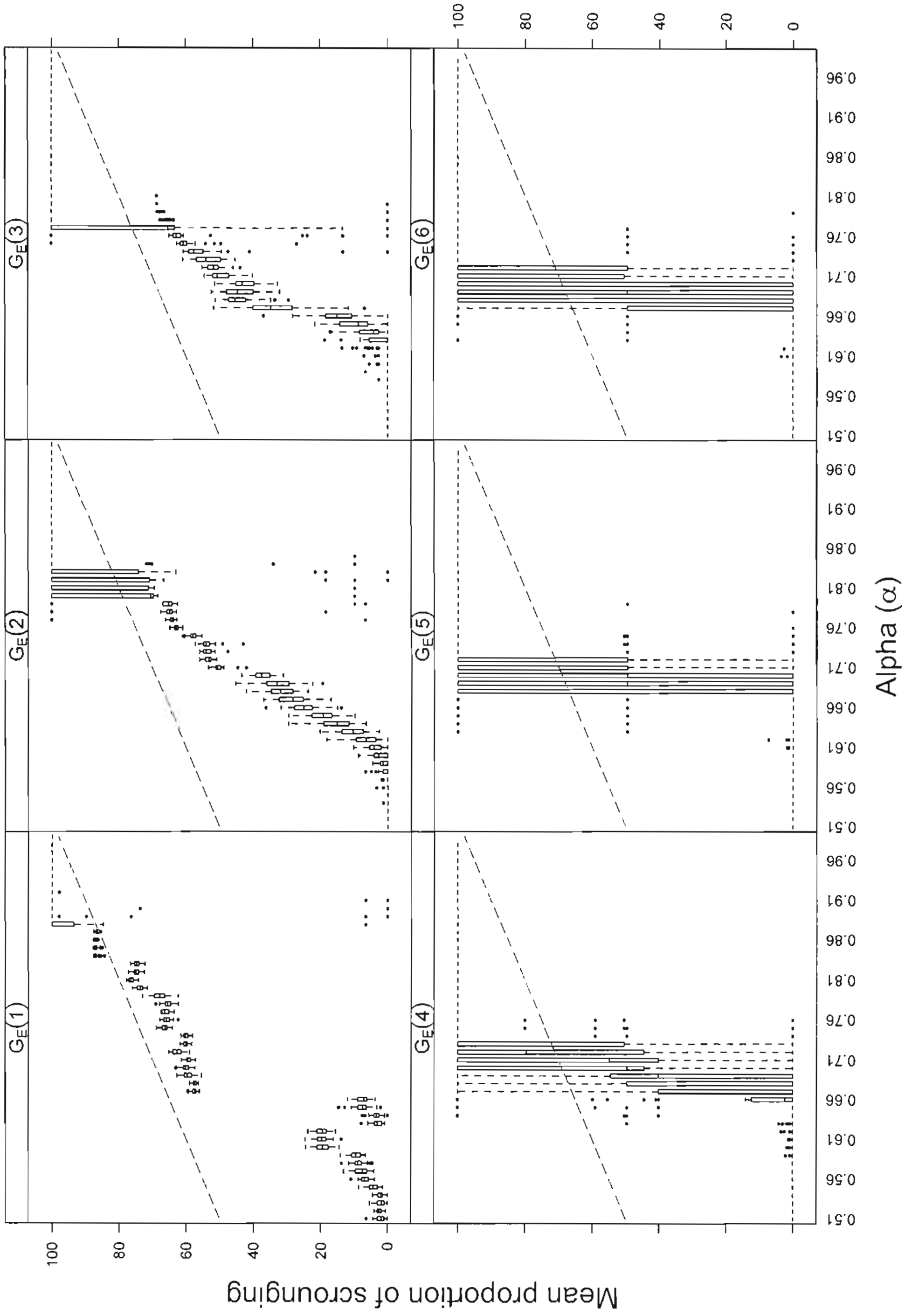

Figure V.4: Mean scrounging values, by value of α and G_E. The dashed line shows the predictions of the deterministic rate-maximizing model for each value of α.

would be analogous to real populations in which social foraging never takes hold because scroungers cannot establish themselves.

V.4.2 Invasion

Figures V.3 and V.4 provide evidence for a mixed stable equilibrium frequency in our model just as in the DRM model, but the existence of an SEF does not mean that populations can reach that SEF. To test whether the social learning rule in our model allows scroungers to establish themselves in a population of producers, we did invasion tests with single scroungers as a function of α and effective group size and plotted the results in Figure V.5.

The results demonstrate that invasion is possible for many values of α, though this effect is once again mediated by the effective group size (section V.4.4). Scroungers typically invade a population of producers in one of two ways: they will either form a colony of a size no greater than the area defined by the effective group size, or the use of the scrounger tactic will spread without bounds and any equilibrium will be an oscillating one over the entire area of the grid. In the case of the former, it is possible to predict how many scroungers can co-exist in the neighbourhood area defined by the radius for a particular effective group size (i.e. 9 squares for a radius of 1). If the area of the radius A_r is $A_r = (2r+1)^2$, where r is the radius, then x scroungers will be stable when

$$(A_r - x - 1) > (A_r \cdot 0.5)/\alpha \tag{V.3}$$

and the maximum number of scroungers in the neighbourhood for a given radius is $(A_r + 1)/2$.

V.4.3 Population dynamics

Two classes of outcomes were seen in this model (Wolfram 2002). The first, stable oscillations, occurred when the entire grid locked into an oscillating pattern (typically with a short period, though we cannot rule out longer period patterns). The second class of outcomes comprised runs which appeared to never reach a stable endpoint, which we call chaotic outcomes. As a subset of the first class of outcome, as noted above the invasion tests would often produce "colonies", small, stable blocks

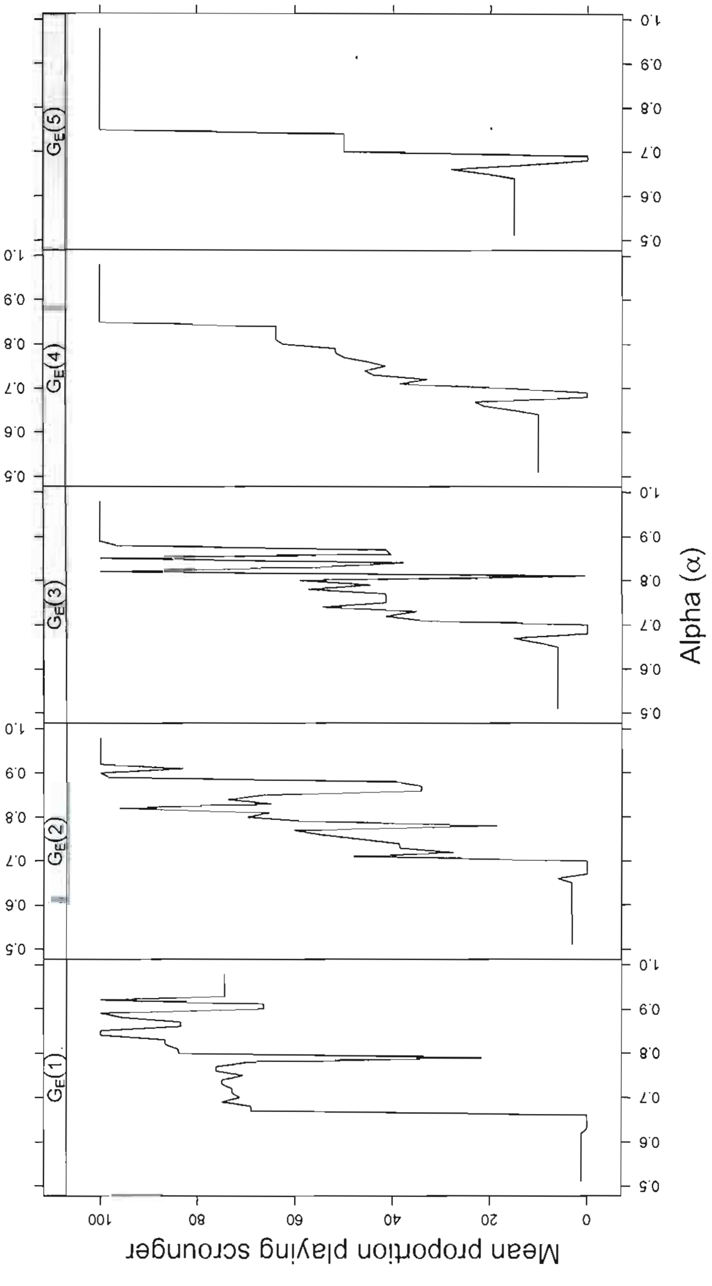

Figure V.5: Invasion by a single scrounger, by α value and effective group size of interaction. When the mean proportion of scrounger is at or near 0%, this indicates that the scrounger was either extinguished or formed a small, stable configuration; values near 100% indicate that scroungers extinguished (or nearly extinguished) producers, and intermediate values suggest chaotic, unpredictable mixed populations of producing and scrounging. Note that there are fewer intermediate values as the effective group size increases.

of scroungers that remained fixed or oscillated in a self-contained group surrounded by producers.

From the invasion tests, we noted that for small values of α, colony outcomes were common and we could predict the size of these colonies from Equation V.3, but as α increased this relationship broke down and scroungers would grow without bounds throughout the entire grid. It is possible to see the form of this pattern in Figure V.5; for example, at the smallest effective group size, colonies arose at α values between 0.5 and 0.62. Following that, mean scrounger values rapidly increased and displayed great variability. In these regions, unpredictable oscillating or chaotic outcomes are the rule, as pictured in Figure V.6, which shows a mixed equilibrium with scroungers scattered throughout the grid. The form of this pattern is similar to the patterns of deterministic chaos found in discrete systems like the logistic map (May 1976) and other cellular automata (Wolfram 2002).

When comparing individual behaviour to population equilibrium values, a startling effect appears. As pictured in Figure V.7, mixed equilibrium outcomes oscillate unpredictably at the level of the individual, such that individual agents may be scroungers one moment or producers the next with no discernible pattern. Blocks of individuals will group together and play producer or scrounger for some time, with these blocks moving across the grid and then being displaced by other formations or swallowed whole, while other individuals remain fixed on one tactic or flip back and forth. However, when we calculate the proportion of the population playing each tactic, the overall values for producer and scrounger remain remarkably stable (allowing for the fluctuations inherent in the fact that the grid is composed of a discrete number of cells). It is also instructive to compare Figure V.7 to the population-level results in Figures V.3 and V.4; chaotic outcomes occur in regions of α values which lead to mixed equilibrium outcomes.

V.4.4 Effective group size

As seen in Figures V.3, V.4 and V.5, the effective group size has a dampening effect on chaotic population equilibrium outcomes. At larger effective group sizes, the intermediate zone where mixed equilibria occur is severely truncated, to the point where only a few values of α lead to the overall co-existence of producing and scrounging behaviours instead of an all-producer or all-scrounger (pathological) population, or

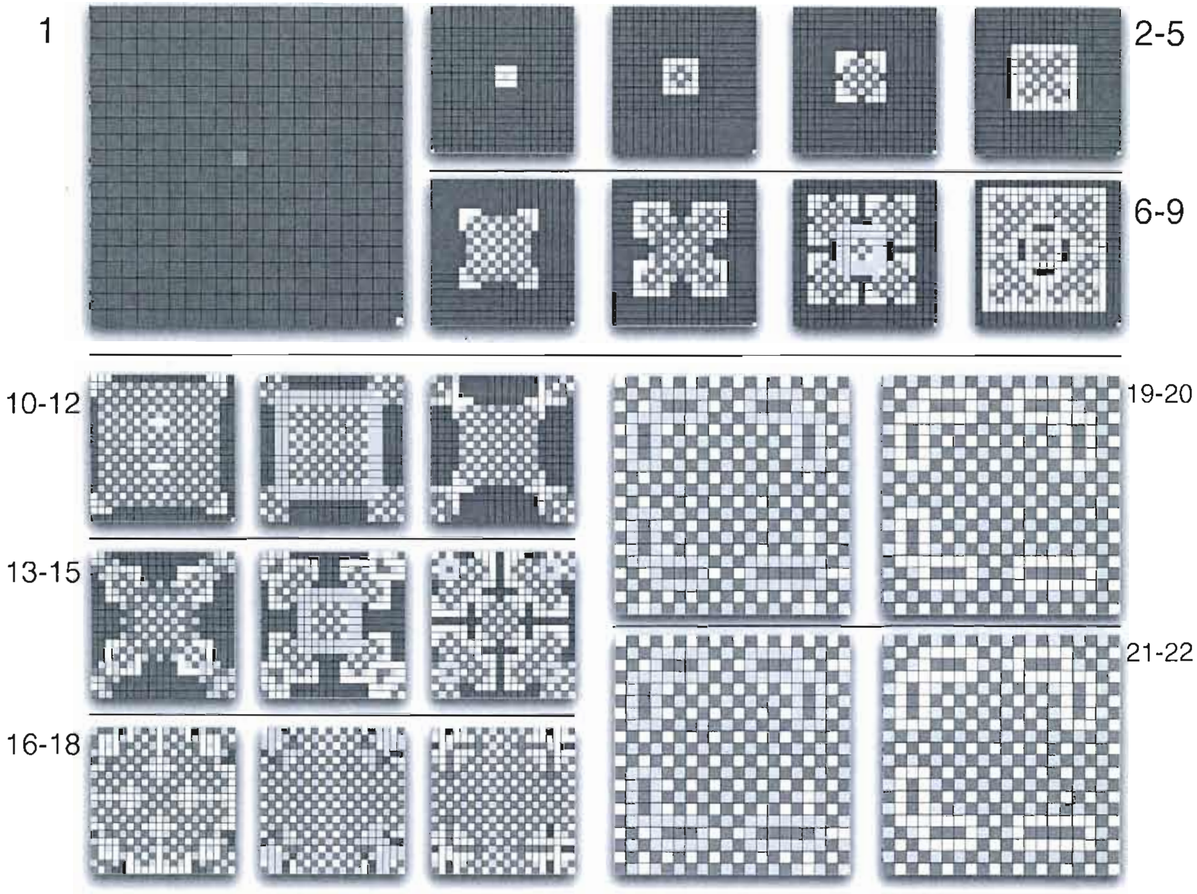

Figure V.6: Invasion by a single scrounger in a population of producers, where the final result is an oscillating equilibrium. Red is a scrounger, blue is a producer, yellow is a scrounger that was a producer in the previous time step, and green is a producer that was a scrounger in the previous time step. Numbers in the margins indicate the order of time steps, starting with 1 in the top left and progressing left to right and top to bottom. In the final four steps shown (19-20, 21-22), the system has settled into a stable oscillation which flips back and forth between two states.

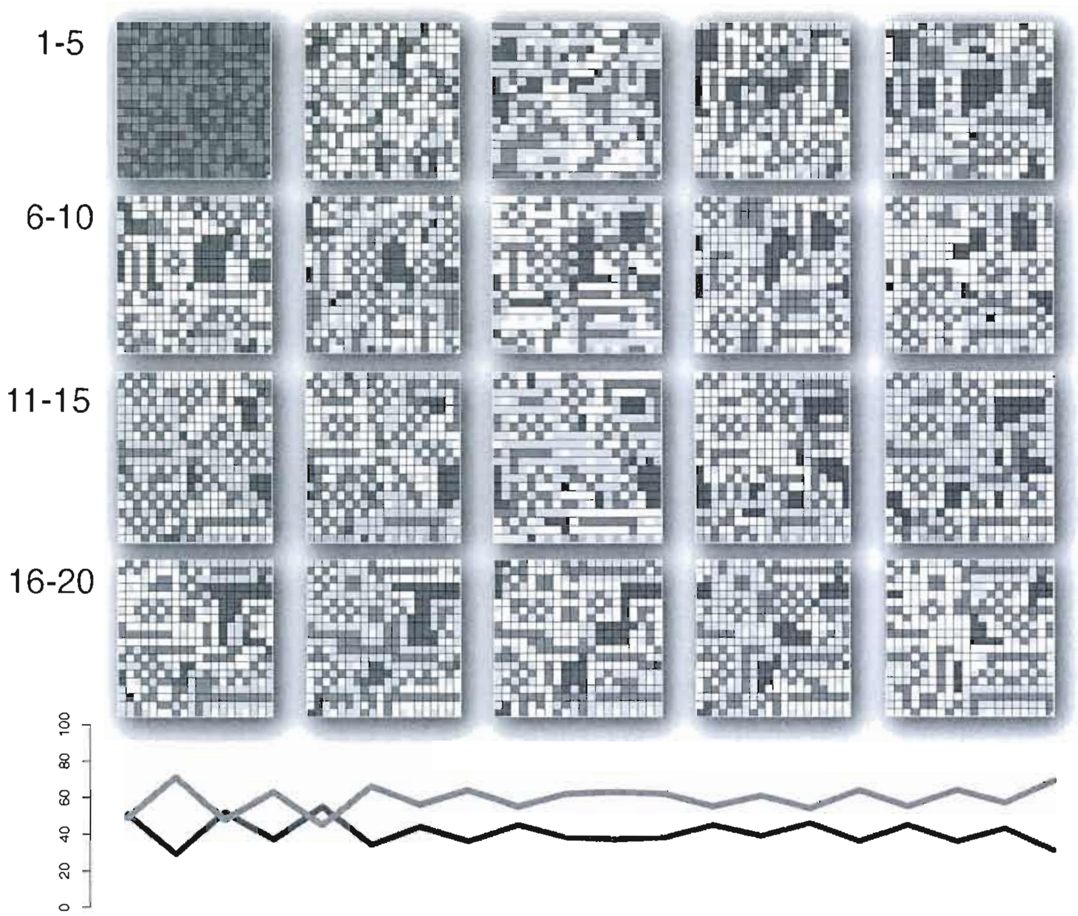

Figure V.7: A chaotic outcome. Shown is the first twenty steps of a run that did not achieve a fixed outcome after 10000 time steps, with the population proportion of scrounger and producer over the twenty steps graphed below. Red is a scrounger, blue is a producer, yellow is a scrounger that was a producer in the previous time step, and green is a producer that was a scrounger in the previous time step; the graph lines include cells that switched, such that the red scrounger line is the total of the red and yellow cells in that step, just as the blue producer line includes the blue and green cells.

individual scrounger colonies. This effect of the social learning model is not seen in the DRM model, where scrounging exists only as a part of a mixed ESS solution. Note that this effect is not explainable simply as an outcome of crowding, because as noted in the methods, grid size was scaled with effective group size to make the neighbourhood of each cell a (relatively) constant proportion of the grid.

V.5 Discussion

The deterministic rate-maximizing (DRM) model predicts a mixed equilibrium outcome for social foraging without specifying a mechanism for how that equilibrium is achieved; classical models assumed a genetic mechanism operated upon by natural selection. By specifying a simple heuristic behaviour rule using social information in a spatially-explicit model, we find unexpected equilibrium outcomes and complex population dynamics in the resulting producer-scrounger game. When comparing to the DRM model, we showed that scrounging increases as the value of α (which has the same effect as the finder's share in the DRM model) increases. However, the effect is non-linear, so that at low values of α the population is much more resistant to scroungers, while at high values of α pathological outcomes that lead to the collapse of social foraging (100% scrounging) are possible. Mixed equilibrium outcomes occur at intermediate values of α, which correspond to populations playing a mixed ESS of the producer and scrounger tactics in the DRM model. Our results also show that for low values of α the invasion of scroungers into a population of producers will often lead to scrounging in isolated colonies within the larger population, an outcome that cannot be derived from any of the classical producer-scrounger models.

Furthermore, these effects are heavily influenced by the effective group size, such that environments with long-range interactions (larger effective group size) have greatly reduced zones of mixed equilibrium outcomes and more all-producer or all-scrounger outcomes. This difference in the effective group size, driven by environmental conditions or phenotypic differences - bird vs. terrestrial animals, for example - could lead to some species foraging socially and others foraging individually (i.e. a population consisting entirely of producers is indistinguishable from a population foraging non-socially). The impact of effective group size on scrounging also suggests that systems with high or low levels of scrounging should have interactions that are highly local (small effective group size) and that social foraging systems with a wide range of patch environments, where the value of α fluctuates as scroungers are able to take a larger or smaller proportion of the food in each patch, would be better supported under highly local interactions. In essence, large effective group sizes have a significant dampening effect on interesting, chaotic outcomes in this producer-scrounger game. This might help to explain why species with similar ecologies may exploit clumped food differently (Maher and Lott 2000); our model suggests that species that have a larger effective group size - which may manifest as more gregarious species, species with greater cognitive or sensory abilities, etc. - would be less likely to have social foraging, while similar species with smaller effective group sizes might have greatly different levels of scrounging despite facing only a small difference in the way that patches are divided. This effect cannot be derived from the DRM model, which predicts a linear relationship between the finder's share and the equilibrium value of scrounging regardless of group size.

The implications of the foraging heuristic also help to solve a largely ignored problem with the DRM model, which is that the classical model requires that animals pay attention to every other member of their foraging group. This remains true no matter how large that group is, because all scroungers must join the patch discovery of every producer and it is an assumption of the DRM model that simultaneous patch discoveries are impossible. Such tracking is likely to be an impossible sensory or cognitive task for any but the smallest groups, but the social learning model also suggests that animals who are foraging socially may be better off paying attention only to animals in a small group anyways. In short, no matter what the absolute group size is a social forager should pay attention only to the nearest neighbours (the effective group size).

Perhaps most importantly, in our model we see that the social learning heuristic employed by foragers ("adopt the tactic that has the highest payoff among all of your neighbours") allows them to use strategies flexibly, changing on a moment-to-moment basis as shown in Figure V.7 while the population usage of each tactic reaches and maintains an equilibrium. The pattern of behaviour observed in our results allows foragers to respond sensibly to changing conditions in their immediate environment while still achieving a population equilibrium; this matches qualitative results seen in flocks of captive nutmeg mannikins (*Lonchura punctulata*; Mottley and Giraldeau 2000). The findings of Coolen and Giraldeau (2003) also align with our results, as they showed that nutmeg mannikins switch between the producer (head-down) and scrounger (head-up) tactics with great rapidity, on the order of 3-5 seconds spent on each tactic. Such flexibility in tactic use is an important issue for theoretical and empirical investigations of foraging behaviour (and strategic decision making in general), but the traditional way of modelling such flexibility has been learning rules (Harley 1981; Hamblin and Giraldeau 2009) which use only personal information obtained by sampling payoffs to tactics. Therefore, the results of our study are an important step towards integrating learning mechanisms into social foraging models. It would be interesting to compare the use of social learning in our model with recent work on mechanisms such as learning rules (Beauchamp 2000; Hamblin and Giraldeau 2009) for personal information; one prediction from the model in Hamblin and Giraldeau (2009) was that producing behaviour should be difficult to extinguish and that this effect became stronger as group size increased, which is similar to the increasingly broad regions of α as G_E grows for which the population is predicted to be composed entirely of producers or scroungers (pathological outcomes). The details of a full comparison, which would require bridging the cellular automaton we use with the individual-based models that have been used to study learning rules, are beyond the scope of this work but the mechanisms of learning personal and social information and their interaction should prove a fruitful avenue of future research (McNamara and Houston 2009).

The model we have discussed in this study also suggests new directions for empirical tests. The local interactions captured in our model resemble the situations commonly seen in empirical work on the producer-scrounger game (e.g. Wu and Giraldeau 2005; Barrette and Giraldeau 2006; Coolen et al. 2007; Mathot and Giraldeau 2008; King et al. 2009), and the predictions of our model should be testable. Comparative analyses might examine social foraging across species with different effective group sizes or an experimental manipulation might be found to test effective group size in lab work, and comparison of the spatial patterns we see in our work (Figures V.6 and V.7, for example) to lab or field systems should be possible if the interactions between foragers can be tracked. The effects that we have predicted from manipulating the value of α as discussed above may also provide new insight into the laboratory and field study of social foragers; most studies to date have assumed the linear relationship between the finder's share found in the DRM model, but the social learning model suggests that there might instead be a non-linear relationship. Experiments with a fine-grained manipulation of the way in which the patch is divided should provide a key test for our model, as does the interaction between effective group size and α. For example, a clear difference between the models can be found at high values of α which result in the breakdown of social foraging in our model, an effect which grows more powerful as effective group size increases; if the amount of the patch that scroungers can take is manipulated toward 100%, our model predicts that producers will do so poorly relative to scroungers because of local interactions that the result will be pathological. This might involve a retreat from social to individual foraging or even a change to a smaller effective group size, which could be tested with methods from network analysis (Croft et al. 2008).

Future work on models like this can take several approaches. Extensions to the basic model we present are certainly possible, as a start: for example, the deterministic updating rule we use might be replaced with a stochastic rule which allows for more complexity at the cost of reproducibility (Moyano and Sánchez 2009), or the effects of different neighbourhood types (Moore vs. von Neumann and others) might be examined. To take the model beyond a cellular automaton and allow for movement of agents, with the corresponding asymmetry in relationships and measurable distance between them, it will likely be necessary to turn back to individual-based models (Beauchamp 2008; Hamblin and Giraldeau 2009), but it can now be done in the light of simpler, more tractable models such as the one we present here.

V.6 Acknowledgments

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V.7 Bibliography

Arbilly, M., Motro, U., Feldman, M. W., and Lotem, A. (2010). Co-evolution of learning complexity and social foraging strategies. *Journal of Theoretical Biology*, 267(4):573–581.

Barnard, C. J. and Sibly, R. M. (1981). Producers and scroungers: A general model and its application to captive flocks of house sparrows. *Animal Behaviour*, 29:543–550.

Barrette, M. and Giraldeau, L.-A. (2006). Prey crypticity reduces the proportion of group members searching for food. *Animal Behaviour*, 71:1183–1189.

Barta, Z., Flynn, R., and Giraldeau, L.-A. (1997). Geometry for a selfish foraging group: a genetic algorithm approach. *Proceedings of the Royal Society of London. Series B, Biological Sciences*, 264:1233–1238.

Bassi, S. (2007). A primer on python for life science researchers. *PLoS Computational Biology*, 3(11):2052–2057.

Beauchamp, G. (2000). Learning rules for social foragers: Implications for the producer-scrounger game and ideal free distribution theory. *Journal of Theoretical Biology*, 207:21–35.

Beauchamp, G. (2001). Consistency and flexibility in the scrounging behaviour of zebra finches. *Canadian Journal of Zoology*, 79:540–544.

Beauchamp, G. (2008). A spatial model of producing and scrounging. *Animal Behaviour*, 76:1935–1942.

Coolen, I. and Giraldeau, L.-A. (2003). Incompatibility between antipredatory vigilance and scrounger tactic in nutmeg mannikins, *Lonchura punctulata. Animal Behaviour*, 66:657–664.

Coolen, I., Giraldeau, L.-A., and Vickery, W. L. (2007). Scrounging behavior regulates population dynamics. *Oikos*, 116:533–539.

Croft, D. P., James, R., and Krause, J. (2008). *Exploring animal social networks.* Princeton University Press, Princeton, NJ.

Dall, S. R. X., Giraldeau, L.-A., Olsson, O., McNamara, J. M., and Stephens, D. W. (2005). Information and its use by animals in evolutionary ecology. *TRENDS in Ecology and Evolution*, 20(4):187–193.

Danchin, É., Giraldeau, L.-A., Valone, T. J., and Wagner, R. H. (2004). Public information: from nosy neighbors to cultural evolution. *Science*, 305:487–491.

Galef, B. G. and Giraldeau, L.-A. (2001). Social influences on foraging in vertebrates: causal mechanisms and adaptive functions. *Animal Behaviour*, 61:3–15.

Giraldeau, L.-A. and Caraco, T. (2000). *Social Foraging Theory.* Monographs in Behavior and Ecology. Princeton University Press, New Jersey.

Giraldeau, L.-A. and Dubois, F. (2008). Social foraging and the study of exploitative behaviour. In Brockmann, H. J., Snowdon, C. T., Roger, T. J., Naquib, M., and Wynne-Edwards, K. E., editors, *Advances in the study of behavior*, volume 38, pages 59–104. Elsevier.

Hamblin, S. and Giraldeau, L.-A. (2009). Finding the evolutionarily stable learning rule for frequency-dependent foraging. *Animal Behaviour*, 78:1343–1350.

Hamblin, S. and Hurd, P. L. (2007). Evolution's strategies: Genetic algorithms and game theory models. *Animal Behaviour*, 74(4):1005–1018.

Harley, C. B. (1981). Learning the evolutionarily stable strategy. *Journal of Theoretical Biology*, 89:611–633.

Harley, C. B. (1987). Learning rules, optimal behaviour, and evolutionary stability. *Journal of Theoretical Biology*, 127:377–379.

Houston, A. I. (1983). Comments on "learning the evolutionarily stable strategy". *Journal of Theoretical Biology*, 105:175–178.

Houston, A. I. and Sumida, B. H. (1987). Learning rules, matching, and frequency dependence. *Journal of Theoretical Biology*, 126:289–308.

King, A. J., Isaac, N. J. B., and Cowlishaw, G. (2009). Ecological, social and reproductive factors shape producer-scrounger dynamics in baboons. *Behavioral Ecology*.

Kurvers, R. H., Prins, H. H., van Wieren, S. E., van Oers, K., Nolet, B. A., and Ydenberg, R. C. (2010). The effect of personality on social foraging: shy barnacle geese scrounge more. *Proceedings of the Royal Society of London. Series B, Biological Sciences*, 277(1681):601–608.

Maher, C. R. and Lott, D. F. (2000). A review of ecological determinants of territoriality within vertebrate species. *American Midland Naturalist*, 143(1):1–29.

Mathot, K. J. and Giraldeau, L.-A. (2008). Increasing vulnerability to predation increases preference for the scrounger foraging tactic. *Behavioral Ecology*, 19(1):131–138.

May, R. M. (1976). Simple mathematical models with very complicated dynamics. *Nature*, 261:459–467.

Maynard Smith, J. (1982). *Evolution and the Theory of Games*. Cambridge University Press, New York, NY.

McNamara, J. M. and Houston, A. I. (2009). Integrating function and mechanism. *Trends in Ecology & Evolution*, 24(12):670–675.

Milinski, M. (1984). Competitive resource sharing: An experimental test of a learning rule for esss. *Animal Behaviour*, 32:233–242.

Morand-Ferron, J. and Giraldeau, L.-A. (2010). Learning behaviorally stable solutions to producer-scrounger games. *Behavioral Ecology*, 21(2):343–348.

Morand-Ferron, J., Giraldeau, L.-A., and Lefebvre, L. (2007). Wild carib grackles play a producer-scrounger game. *Behavioral Ecology*, 18(5):916–921.

Mottley, K. and Giraldeau, L.-A. (2000). Experimental evidence that group foragers can converge on predicted producer-scrounger equilibria. *Animal Behaviour*, 60:341–350.

Moyano, L. G. and Sánchez, A. (2009). Evolving learning rules and emergence of cooperation in spatial prisoner's dilemma. *Journal of Theoretical Biology*, 259:84–95.

Nowak, M. (1990). An evolutionarily stable strategy may be inaccessible. *Journal of Theoretical Biology*, 142:237–241.

Nowak, M. A. (2006). *Evolutionary Dynamics: Exploring the Equations of Life.* Harvard University Press, Cambridge, Massachusetts.

Nowak, M. A. and May, R. M. (1992). Evolutionary games and spatial chaos [letter to the editor]. *Nature*, 359(4):826–829.

Rapoport, A. and Guyer, M. (1966). A taxonomy of 2 x 2 games. *General Systems*, 11:203–214.

Rendell, L., Boyd, R., Cownden, D., Enquist, M., Eriksson, K., Feldman, M. W., Fogarty, L., Ghirlanda, S., Lillicrap, T., and Laland, K. N. (2010). Why copy others? insights from the social learning strategies tournament. *Science*, 328:208–213.

Selten, R. and Hammerstein, P. (1984). Gaps in harley's argument on evolutionarily stable learning rules and in the logic of "tit for tat". *Behavioral and Brain Sciences*, 7:115–116.

Steele, W. K. and Hockey, P. A. R. (1995). Factors influencing rate and success of intraspecific kleptoparasitism among Kelp gull (*Larus dominicanus*). *The Auk*, 112(4):847–859.

Stephens, D. W. and Krebs, J. R. (1986). *Foraging theory.* Monographs in Behavior and Ecology. Princeton University Press, New Jersey.

Tracy, N. D. and Seaman Jr., J. W. (1995). Properties of evolutionarily stable learning rules. *Journal of Theoretical Biology*, 177:193–198.

Vickery, W. L., Giraldeau, L.-A., Templeton, J. J., Kramer, D. L., and Chapman, C. A. (1991). Producers, scroungers, and group foraging. *The American Naturalist*, 137(6):847–863.

Wolfram, S. (1984). Cellular automata as models of complexity. *Nature*, 311(4):419–424.

Wolfram, S. (2002). *A new kind of science.* Wolfram Media.

Wu, G.-M. and Giraldeau, L.-A. (2005). Risky decisions: a test of risk sensitivity in socially foraging flocks of lonchura punctulata. *Behavioural Ecology*, 16(1):8–14.

CHAPTER VI

LANDSCAPE GEOMETRY AND PRODUCER-SCROUNGER

Preamble

This chapter is an article in preparation for submission (potential journals include *Proceedings of the Royal Society, Series B* or *Behavioral Ecology*). Steven Hamblin was responsible for the entire study.

A model of landscape geometry for producing and scrounging

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VI.1 Abstract

The producer scrounger game is a model of social foraging, wherein an animal's foraging success is contingent on it's own choices and the choices of others simultaneously. The model assumes that individuals invest time in finding resources (producing) or joining resource discoveries (scrounging). The model has been productive theoretically and empirically, but the generalization of the the theory and laboratory work to more realistic animal foraging is hampered by the nature of landscapes upon which foragers have been studied to date. In this study I present a model that takes the underlying landscape geometry (the way space is represented, usually as a square grid) into account and demonstrates that by manipulating this geometry to be more realistic we can significantly affect the outcomes in the producer-scrounger game. I use these results to argue that future work must take landscape effects into account if research on the producer-scrounger paradigm is to be successfully applied to real animal foragers in the specific and to systems of exploitation in general.

VI.2 Introduction

The study of social foraging - in which a forager's decisions are directly related to the decisions of other foragers under conditions of frequency dependence - has been represented most successfully by the body of theory and empirical work known as the producer-scrounger game (Barnard and Sibly 1981; Giraldeau and Caraco 2000; Giraldeau and Dubois 2008). In this game, individuals may adopt one of two tactics, producer or scrounger. Producers invest time in searching for resources (e.g. food patches), while scroungers join the discoveries of producers but do not search themselves. A strategy in the producer-scrounger game is a mix of producing and scrounging contingent on the actions of other foragers in the group (a mixed strategy); the producer-scrounger game has a solution in the form of an evolutionarily stable strategy (ESS: Maynard Smith 1982) in which individuals produce some proportion of the time and scrounge the rest. The producer-scrounger game has been productive both theoretically and empirically (reviewed most recently in Giraldeau and Dubois 2008). Many species have been observed behaving in accordance with the producer-scrounger model: a non-exhaustive list includes such diverse species as bald eagles (Hansen 1986), shark mackerel (Auster 2008), zebra finches and nutmeg mannikins (Giraldeau et al. 1990), Harris' sparrows (Rohwer and Ewald 1981), kelp gulls (Steele and Hockey 1995), pigeons (Giraldeau and Lefebvre 1986), baboons (King et al. 2009), barnacle geese (Kurvers et al. 2010) and pigs (Held et al. 2000). More generally, the game applies in situations beyond foraging to broader questions where parasitic exploitation of (non-food) resources occurs (Barnard 1984; Giraldeau and Dubois 2008)

Yet to date, almost all of the experimental laboratory work testing predictions or variations of the producer-scrounger model has been on small birds, grouped into flocks numbering no more than 6 or 8 in an aviary in which birds forage on grids populated by regularly-spaced patches of food (e.g. Giraldeau et al. 1990; Koops and Giraldeau 1996; Mottley and Giraldeau 2000; Coolen et al. 2001; Katsnelson et al. 2008; Mathot and Giraldeau 2008; Morand-Ferron and Giraldeau 2010). These aviaries bear little resemblance to the foraging landscape faced by birds such as the zebra finch (Zann 1996), where patches are dotted in a landscape with heterogenous geometries that sized much differently (usually larger) than laboratory aviaries. Similarly, simulation studies have sought to extend producer-scrounger theory (e.g. Barta et al. 1997; Beauchamp and Giraldeau 1996; Beauchamp 2000; 2008; Hamblin and Giraldeau 2009; Hamblin et al. 2009; Kurvers et al. 2011), but these have all used the same landscape format as found in aviary work: simulated foragers interact with each other across a regular, square grid, a spatial environment that is entirely homogenous.

Other authors have made clear and compelling arguments that landscape features and spatial heterogeneity matter to animal behaviour (Turner 1989; Johnson et al. 1992), but we know little of how these processes affect animals engaged in a producer-scrounger game. For instance, foragers in a producer-scrounger system must travel through their environment to search for patches (search time) and join patch discoveries (travel time) before the patches are depleted, but these effects have received little attention; theoretical work avoids mention of spatial processes (one exception found in Beauchamp 2008), and empirical work is done in spaces which are highly restricted. Adding explicit spatial representations and processes to current theoretical work has the potential to significantly enhance the external and ecological validity of these models.

Addressing this concern by conducting large-scale laboratory work on social foragers with more complex environments would be ideal, but such experiments remain out of reach as yet. Therefore, this study presents a simulation model that explicitly manipulates landscape geometry upon which foragers playing a producer-scrounger game interact. Following Holland et al. (2007), I test the effects of four landscape geometries (von Neumann, hexagonal, Moore, and Dirichlet, also known as Voronoi; see Figure VI.1) on producer-scrounger outcomes. This study distinguishes between the effect of regular grids (von Neumann, hexagonal, and Moore) which are characterized by their fixed number of neighbours and fixed patch sizes and the irregular Dirichlet grid, with its variable number of neighbours and mix of large and small patches. Of particular note are Moore grids, the most commonly used geometry in simulation work, and the heterogenous Dirichlet grid, which more closely resembles real landscapes that animals might encounter. The effects of these geometries are measured by outcomes including ESS values of scrounging, feeding rates, and flock geometry, to allow insight into the mapping of producer-scrounger models to real landscapes.

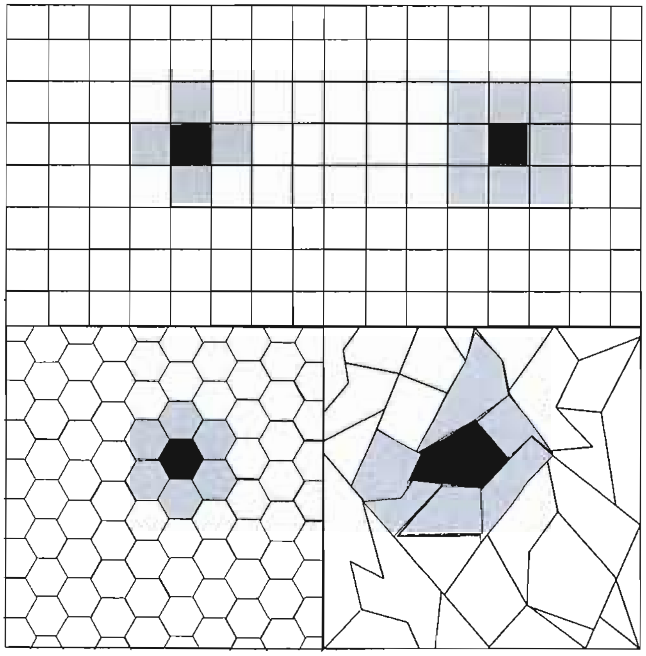

Figure VI.1: Landscape geometries modelled in this study, with neighbourhoods for each patch (black) indicated in grey. Clockwise from top-left: von Neumann (4 neighbours per patch), Moore (8 neighbours), Dirichlet (variable), and hexagonal (6 neighbours).

VI.3 Methods

To model the effect of landscape geometry, I used an individual-based model (IBM). Individuals played a producer-scrounger social foraging game on a grid with n_p patches (see Table VI.1) and population size was scaled as a percentage n_f of n_p. For this study, n_p was held constant at 400, and so $n_f = 5(\%)$ was a population of 20 foragers. In any given round, n_{pf} patches held food items, measured as a percentage of n_p; $n_{pf} = 10$ means that 10% of the patches were filled, and to avoid the effects of patch depletion n_{pf} was held constant by randomly regenerating filled patches as they were exhausted. Each patch contained 20 food items; Kurvers et al. (2011) found that in a spatial producer-scrounger model patch richness had significant effects on the equilibrium value of scrounging, and so we kept the number of items in each patch constant to explore the effects of the other variables.

The grid geometry was manipulated by changing the number of neighbours for each patch; in the von Neumann, hexagonal, and Moore grid geometries, each patch had a regular number of neighbours (4, 6, and 8 respectively), while in the Dirichlet geometry each patch had a variable number of neighbours, constructed so as to have a mean of 6, s.d. of 1.8, and range 2-12 neighbours. Grids were represented in code as a graph object, and Dirichlet geometries were constructed by an algorithm written by the author after descriptions such as those found in Green and Sibson (1978). The code for this simulation was written in Python and is available upon request.

At each time step if they were not feeding or moving, individuals chose to scrounge with probability p_s or produce with probability $1 - p_s$. Producers searched their current patch for food, and if no food was discovered, moved between patches by choosing randomly among the neighbouring patches and selected their tactic again in the next round. If food was present in a patch, producers foraged at the patch, removing 1 food item per round, until the patch was exhausted. Scroungers searched the grid for producers and moved towards the nearest producer at the rate of two patches per turn; this was meant to reflect laboratory observations of scrounging individuals and is common in producer-scrounger simulations (e.g. Beauchamp 2008; Hamblin and Giraldeau 2009). If the patch was exhausted before the scrounger arrived, the agent abandoned the attempt and chose their tactic anew in the next round. Upon reaching the patch, scroungers joined the discovery and fed at a rate of 1 unit per round; agents feeding at a patch moved randomly as above in the round after exhausting it.

Foragers received an initial energy budget of $e = 100$ units of energy, and each step of movement depleted e. Foragers who reached $e = 0$ were considered to be "dead" and no longer moved or foraged. I manipulated two aspects of this energy depletion. In the first manipulation, food eaten during foraging would either regenerate energy stores at the rate of one unit of energy per unit of food eaten, or it would have no effect on energy stores (regenerate: false). In the second manipulation, I scaled the energy cost of movement by the number of neighbours for a given patch, under the assumption that patch size would scale linearly with the number of neighbouring patches (larger patches, more neighbours). To normalize the costs around 1, I used the ratio of the number of neighbours for a patch to the median number of neighbours in every patch. Because the von Neumann, Moore, and hexagonal geometries each have a regular number of neighbours, the cost to movement under this scaling remained 1 while the cost varied under the Dirichlet geometry. Analysis of the results (not shown) confirm that foragers under the no regeneration condition with scaling of movement costs (NR-S) had the lowest energy reserves at the end of the simulations, and final energy reserves increased through the NR-NS (no regeneration, no scaling), R-S (regeneration, scaling) and finally R-NS (regeneration, no scaling) conditions as would be expected.

Each run of the the foraging simulation lasted 500 time steps, and I recorded food intake rates to each tactic and flock geometry (I use the language for the birds which have been the favoured subject of producer-scrounger studies, but the term is interchangeable with the more general 'group'). Flock geometry was measured as the mean area of convex hull which encompassed the foraging flock at each time step, averaged over the entire simulation. I varied n_f, n_{pf}, regeneration (T/F) and scaling (T/F) as in Table VI.1 for a total of 240 parameter combinations, and for each combination I systematically varied p_s from 0 to 1 by 0.01 to calculate ESS proportions of tactic use. Each combination of parameters and p_s was replicated 100 times, for a total of 2.4 million runs.

ESS values of tactic use ($\hat{p}_s$) were calculated by comparing the mean intake rates to each tactic during a run and averaged over all 100 replications. The value of p_s at which the intake rates were equal was considered to be the ESS value of scrounging. To automate the calculation of ESS values, I calculated the intake rates to each tactic (producer and scrounger) as a function of p_s for each parameter combination and fit a smoothing cubic spline to the resulting curve for each tactic in R (R Development Core Team 2007). The intersection point of the two curves was calculated by minimizing the squared difference between the curves using R's *optimize* function. In subsequent analyses of food intake and flock geometry, I used the subset of the data formed by taking the runs done at the ESS value of $\hat{p}_s$ for each combination of parameters (24000 runs).

Variable	Description	Values
Grid type	Underlying grid geometry.	{Dirichlet, von Neumann, Moore, hexagonal}
n_p	Number of patches on the grid	400
n_f	Population size (number of foragers) in percent of n_p.	{5,10,20 }
f	Number of food items in each patch.	20
n_{pf}	Number of filled patches, as a percentage of n_p.	{5,10,15,20,25 }
e	Forager energy reservers.	initial value: 100
p_s	Probability of scrounging.	[0, 1]
Regenerate	Boolean: did energy stores replenish when food was eaten?	{True, False}
Scaling	Boolean: did movement costs scale with patch size?	{True, False}

Table VI.1: Model parameters and the values used for this study.

VI.4 Results

Figure VI.2 shows the ESS value of scrounging calculated for each combination of grid type, patch density (n_{pf}), population size (n_f), regeneration (T/F) and cost scaling (T/F). The ESS values showed clear effects from each variable. Scrounging tended to be highest under the Dirichlet geometry and lowest under the von Neumann, though this effect interacted with the other variables. As patch density increased, scrounging decreased (c.f. Figure 1 of Kurvers et al. 2011, where a similar effect was found). Interestingly, scrounging was lowest in the NR-S (no-regeneration but cost-scaled) condition and highest in the R-NS and R-S conditions, suggesting that the ESS value of scrounging was sensitive to the energy budget available (highest under R-NS, lowest under R-S). Population size decreased the variance in scrounging values at high patch densities.

Range	Number of combinations
< 0.05	8
0.05 up to 0.10	33
0.10 up to 0.15	11
0.15 to 0.23	8
Total	60

Table VI.2: Range of ESS values between grid types within each parameter combination, calculated by subtracting the lowest ESS value from the highest.

Figure VI.3 shows the feeding rates by grid type and combinations of patch density and population size, grouped by regeneration and scaling. The effects on the ESS values for each combination of parameters can be seen in this figure: grid type had no consistent effect on feeding rates, but there was a significant increase in intake rates as patch densities went up, and there were also significant differences as a function of energy budget. Feeding rates went down between NR-NS condition (lowest energy reserves) and the R-NS (highest energy reserves). This result follows from the relationship in Figure VI.2, where the NR-S condition had the lowest scrounging and the R-NS and R-S conditions had the highest, and fits with the predictions of producer-scrounger theory that under frequency-dependent foraging mean intake rates go down as the proportion of scrounging in the population increases. There was no clear effect of patch density.

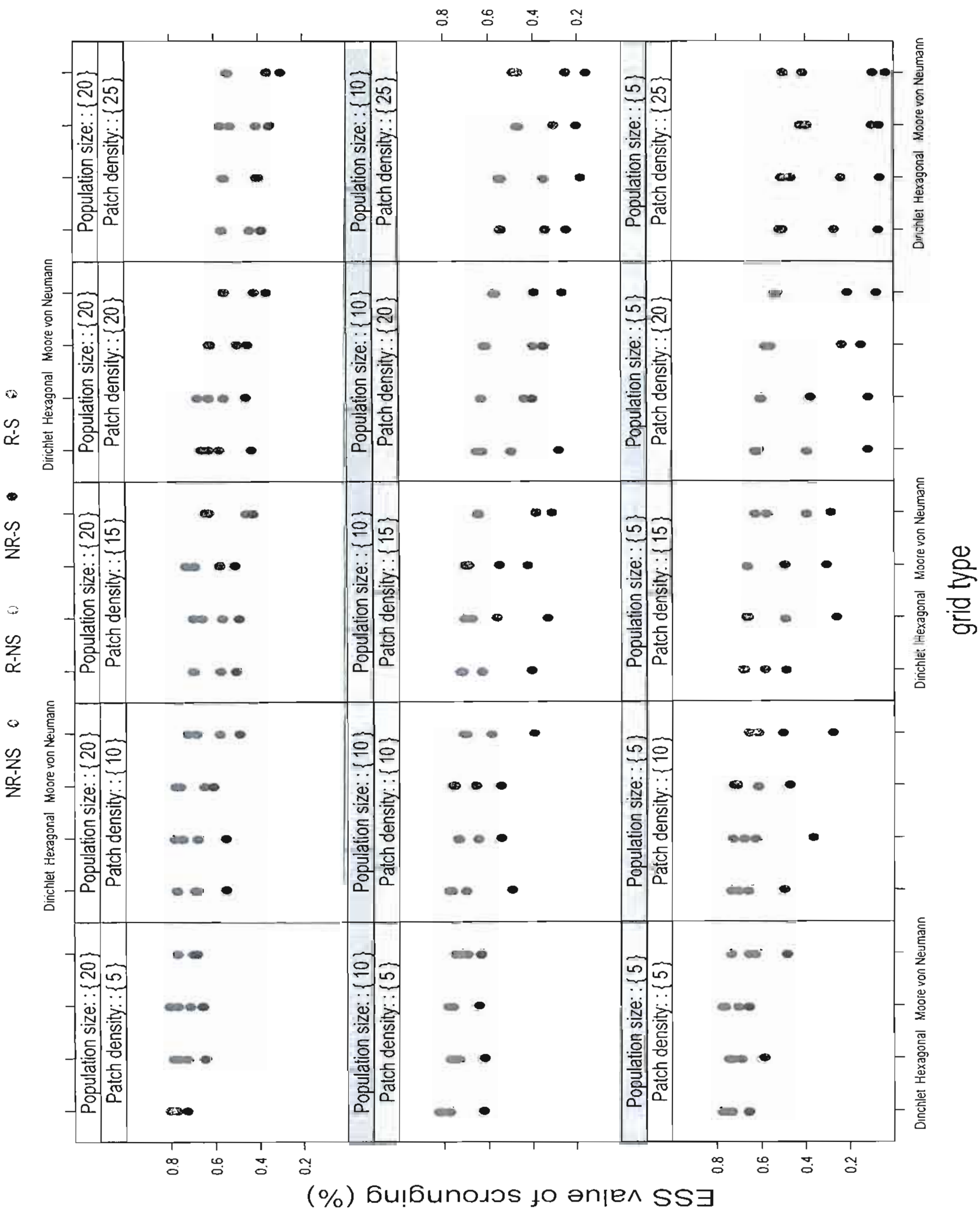

Figure VI.2: ESS values for each parameter combination.

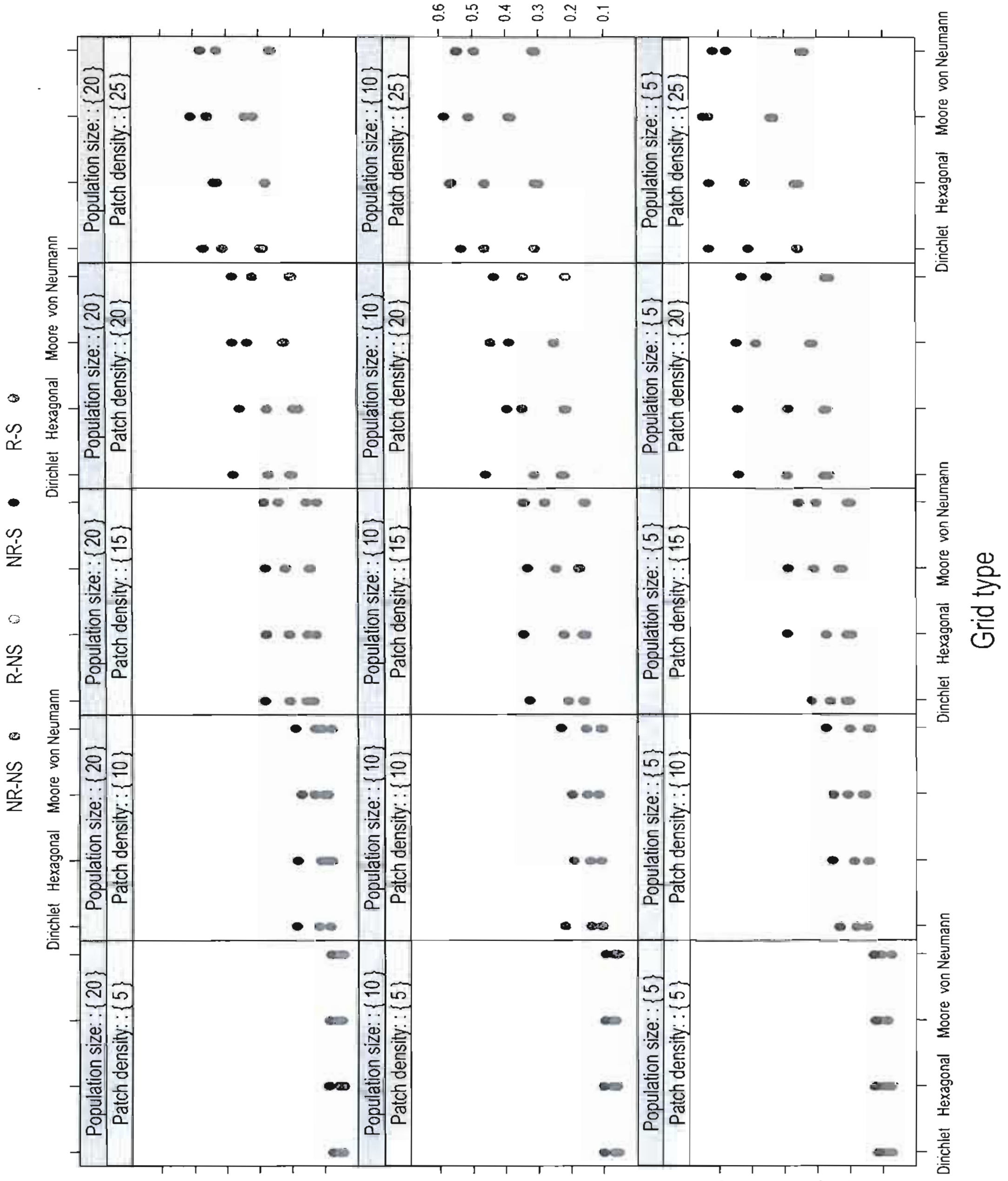

Figure VI.3: Feeding rates (unit food per unit time) for each grid and parameter combination; points are means of 100 replications.

Figure VI.4 shows mean flock area by grid type and combinations of patch density and population size, grouped by regeneration and scaling. Flock geometry showed significant effects of grid type, with flocks being significantly larger (more widely-spaced) under the Dirichlet landscape; the other three geometries showed roughly equal flock areas, and flock geometries grew larger with increased population size and patch density. Once again, grouping by energy budget shows significant effects: lower energy reserves led to larger flock areas and vice versa. Increasing population sizes increased mean flock area.

VI.5 Discussion

The results of the simulation model presented in this study show that the form of the landscape upon which animals forage may have significant and unrecognized effects on the dynamics of the producer-scrounger game. As depicted in Figure VI.2, the ESS values changed as a function of grid type, with differences ranging up to 23% and Table VI.2 shows that a third of the parameter combinations resulted in a difference greater than 10%. Flock geometry showed significant effects of grid type as well, as can be seen in Figure VI.4. Some of these differences are explainable by the ESS value of scrounging for each grid; Barta et al. (1997) show that the area occupied by a flock varies inversely with scrounging, such that producer-only flocks have the largest areas. Indeed, comparing Figure VI.2 to Figure VI.4, combinations with lower ESS values of scrounging had larger areas. However, the size of the difference between the regular (von Neumann, hexagonal, and Moore grids) and irregular (Dirichlet) geometries cannot be explained by ESS values alone and provides strong evidence that the variable geometry of real landscapes may have important effects on the behaviour of animals foraging socially. Also, for both the flock geometries predicted by Barta et al. (1997) and the spatial arrangement of producers and scroungers shown in Kurvers et al. (2011), predation was required to maintain group cohesion, while no such mechanism was required in this model.

The larger flocks (and often higher use of scrounging) in Dirichlet landscapes are likely a consequence of the irregular nature of this landscape. As Holland et al. (2007) demonstrated, the path between two points in irregular landscapes like the Dirichlet is longer than in regular grids. Irregular geometries such as the Dirichlet could

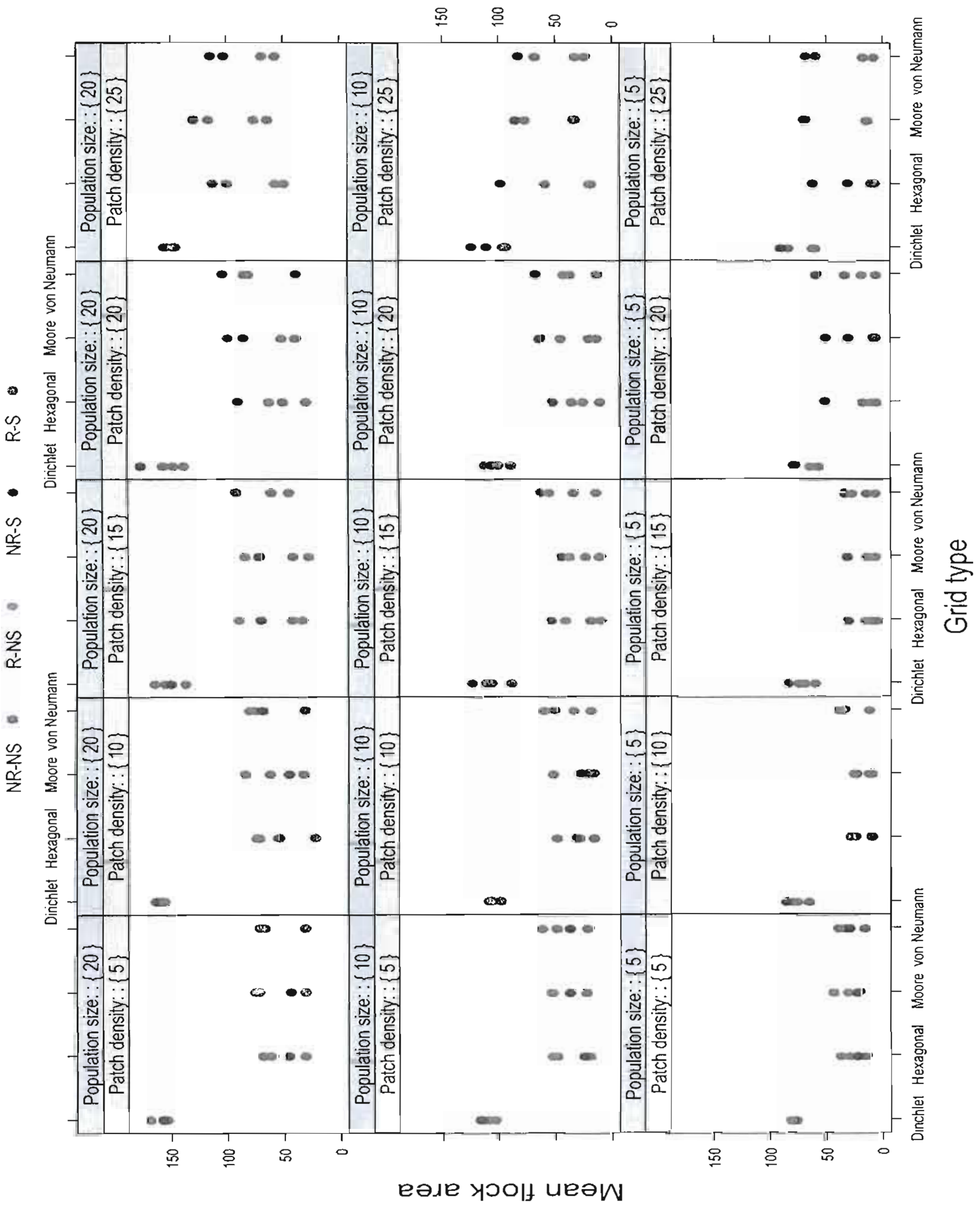

Figure VI.4: Mean flock area for each grid and parameter combination; points are means of 100 replications.

plausibly arise whenever animals are foraging in spatially heterogenous territories (rocky, patchy landscapes with irregular routes between patches, wooded areas with elevation differences, etc.), or as the outcome of group interactions. Few studies to date have explicitly discussed this, but an example is the work done by Doncaster and Woodroffe (1993), who showed that the boundaries of badger setts fit the pattern of a Dirichlet tessellation. Our results are the first I know of to suggest that animals playing producer-scrounger games in such complex conditions will forage in groups with larger areas unless reigned in by other forces like predation or visibility. Future tests of producer-scrounger games in more ecologically realistic environment may be able to manipulate these forces to see if flock geometry changes as a result.

Feeding rates (Figure VI.3) did not show significant differences by grid type and only weak effects from population size, but did show consistent and strong effects from patch density, energy regeneration and cost scaling. The results for both feeding rates and ESS values of scrounging show a clear pattern based on energy reserves: intake rates decreased and scrounging increased as energy reserves increased. The results for patch density inverted this relationship: intake rates increased and scrounging decreased as patch density increased. Patch density's effects on intake and scrounging agree with the results in Kurvers et al. (2011) without the confounding personality variable and confirm the role of patch density as a spatial driver of producer-scrounger dynamics. On the other hand, the effect of energy reserves agrees (qualitatively) with the predictions of variance-sensitive models of producing and scrounging, which predict that scrounging should increase as energy reserves increase (because scrounging has less variance in payoff Stephens 1981; Caraco and Giraldeau 1991). However, these models usually presume that the change in scrounging is a strategic choice made by foragers, such as: "increase scrounging when my energy reserves exceed a threshold x". The same trend in our results comes entirely from the spatially explicit nature of the model; no strategic choice is made by foragers other than maximizing rate of intake by using ESS values of scrounging (as opposed to minimizing the chance of shortfall as in the variance-sensitive models). This model thus suggests a potential link between variance-sensitive producer-scrounger games and spatial processes.

The results presented here should not be seen as an attempt to exhaustively catalogue the effects of landscape geometry or spatial effects (like patch density); they are instead an argument that these effects may significantly affect the predictions of the basic producer-scrounger models and should be taken into account when designing future empirical work. Though full-scale explorations of these processes in laboratory work may not yet be achievable, it should still be possible to manipulate the arrangement of patches under aviary conditions to look for the effects predicted here. Introducing spatial heterogeneity by placing various obstacles on foraging grids, for example, is an easy manipulation that could mimic more realistic landscapes. It may also be possible to detect these effects in field work. In their excellent study of baboons in central Namibia foraging under a producer-scrounger game, King et al. (2009) did not explicitly note the geometry of their desert "small-patch" and woodland "large-patch habitats", but their descriptions sound tantalizingly similar to the difference between regular and irregular grid types and their finding of a 14 times increase in scrounging in the large-patch environment is reminiscent of the differences seen in Figure VI.4. Such systems may provide a good opportunity to test the effects of landscape geometry that are predicted in this study.

The reach of this effect also extends well beyond food-based foraging problems to the logic of exploitation in other systems like mating and social structure. For example, Fukuyama (1991) suggested that the male Japanese foam-nesting frogs he studied played a producer-scrounger game while attempting to mate (here, calling and satellite males are producers and scroungers respectively); further, the description of the conditions under which the frogs mate suggest that these landscape effects might play an important role. Similarly, Winterhalder (1996a; 1997; 1996b) explored producer-scrounger dynamics that might underlie aspects of resource transfers in primates, hominids, and even hunter-gatherer societies, and the question of how these transfers might be structured spatially

As noted in the introduction, a wide variety of species have been found to play the producer-scrounger game when foraging in social groups (and in other, more general situations of exploitation). These species often forage in environments far removed from the aviaries in which the predictions of the producer-scrounger model have been tested on small birds, and the results of this paper provide an argument that these differences can not be ignored if the study of social foraging is to successfully generalize to animals foraging on real landscapes and provide greater understanding of the mechanisms underlying social foraging processes as well as the evolutionary pressures brought to bear on social foragers by their environments. Thus I urge future work on this paradigm to include the effect of spatial heterogeneity and other spatial processes as a first-class citizen when designing and executing new research on social foraging problems.

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VI.7 Bibliography

Auster, P. (2008). Variation in search and predatory attack strategies of shark mackerel *Grammatorcynus bicarnatus. Journal of the Marine Biological Association of the United Kingdom*, 88(4):847–849.

Barnard, C. J. (1984). *Producers and scroungers : Strategies of exploitation and parasitism.* Chapman & Hall, London.

Barnard, C. J. and Sibly, R. M. (1981). Producers and scroungers: A general model and its application to captive flocks of house sparrows. *Animal Behaviour*, 29:543–550.

Barta, Z., Flynn, R., and Giraldeau, L.-A. (1997). Geometry for a selfish foraging group: a genetic algorithm approach. *Proceedings of the Royal Society of London. Series B, Biological Sciences*, 264:1233–1238.

Beauchamp, G. (2000). Learning rules for social foragers: Implications for the producer-scrounger game and ideal free distribution theory. *Journal of Theoretical Biology*, 207:21–35.

Beauchamp, G. (2008). A spatial model of producing and scrounging. *Animal Behaviour*, 76:1935–1942.

Beauchamp, G. and Giraldeau, L.-A. (1996). Group foraging revisited: Information sharing or producer-scrounger game? *The American Naturalist*, 148(4):738–743.

Caraco, T. and Giraldeau, L.-A. (1991). Social foraging: Producing and scrounging in a stochastic environment. *Journal of Theoretical Biology*, 153:559–583.

Coolen, I., Giraldeau, L.-A., and Lavoie, M. (2001). Head position as an indicator of producer and scrounger tactics in a ground-feeding bird. *Animal Behaviour*, 61:895–903.

Doncaster, C. P. and Woodroffe, R. (1993). Den site can determine shape and size of badger territories: implications for group living. *Oikos*, 66(1):88–93.

Fukuyama, K. (1991). Spawning behaviour and male mating tactics of a foam-nesting treefrog, *Rhacophorus schlegelii. Animal Behaviour*, 42:193–199.

Giraldeau, L.-A. and Caraco, T. (2000). *Social Foraging Theory.* Monographs in Behavior and Ecology. Princeton University Press, New Jersey.

Giraldeau, L.-A. and Dubois, F. (2008). Social foraging and the study of exploitative behaviour. In Brockmann, H. J., Snowdon, C. T., Roger, T. J., Naquib, M., and Wynne-Edwards, K. E., editors, *Advances in the study of behavior*, volume 38, pages 59–104. Elsevier.

Giraldeau, L.-A., Hogan, J. A., and Clinchy, M. J. (1990). The payoffs to producing and scrounging: What happens when patches are divisible? *Ethology*, 85:132–146.

Giraldeau, L.-A. and Lefebvre, L. (1986). Exchangeable producer and scrounger roles in a captive flock of feral pigeons: a case for the skill pool effect. *Animal Behavior*, 34(797-803).

Green, P. J. and Sibson, R. (1978). Computing dirichlet tesselations in the plane. *The Computer Journal*, 21(2):168–173.

Hamblin, S. and Giraldeau, L.-A. (2009). Finding the evolutionarily stable learning rule for frequency-dependent foraging. *Animal Behaviour*, 78:1343–1350.

Hamblin, S., Mathot, K. J., Morand-Ferron, J., Nocera, J. J., Rieucau, G., and Giraldeau, L.-A. (2009). Predator inadvertent social information use favours reduced clumping of its prey. *Oikos*, 119(2):286–291.

Hansen, A. J. (1986). Fighting behavior in bald eages: A test of game theory. *Ecology*, 67(3):787–797.

Held, S., Mendl, M., Devereucx, C., and Byrne, R. W. (2000). Social tactics of pigs in a competitive foraging task: the 'informed forager' paradigm. *Animal Behaviour*, 59(569-576).

Holland, E. P., Aegerter, J. N., Dytham, C., and Smith, G. C. (2007). Landscape as a model: The importance of geometry. *PLoS Computational Biology*, 3(10):1979–1992.

Johnson, A. R., Wiens, J. A., Milne, B. T., and Crist, T. O. (1992). Animal movements and population dynamics in heterogeneous landscapes. *Landscape Ecology*, 7(1):63–75.

Katsnelson, E., Motro, U., Feldman, M. W., and Lotem, A. (2008). Early experience affects producer-scrounger foraging tendences in the house sparrow. *Animal Behaviour*, 75:1465–1472.

King, A. J., Isaac, N. J. B., and Cowlishaw, G. (2009). Ecological, social and reproductive factors shape producer-scrounger dynamics in baboons. *Behavioral Ecology*.

Koops, M. A. and Giraldeau, L.-A. (1996). Producer-scrounger foraging games in starlings: A test of rate-maximizing and risk-sensitive models. *Animal Behaviour*, 51:773–783.

Kurvers, R. H., Hamblin, S., and Giraldeau, L.-A. (2011). Scroungers are shy and producers are either: The co-evolution of boldness and alternative foraging tactics. Submitted to *Behavioral Ecology*.

Kurvers, R. H., Prins, H. H., van Wieren, S. E., van Oers, K., Nolet, B. A., and Ydenberg, R. C. (2010). The effect of personality on social foraging: shy barnacle geese scrounge more. *Proceedings of the Royal Society of London. Series B, Biological Sciences*, 277(1681):601–608.

Mathot, K. J. and Giraldeau, L.-A. (2008). Increasing vulnerability to predation increases preference for the scrounger foraging tactic. *Behavioral Ecology*, 19(1):131–138.

Maynard Smith, J. (1982). *Evolution and the Theory of Games*. Cambridge University Press, New York, NY.

Morand-Ferron, J. and Giraldeau, L.-A. (2010). Learning behaviorally stable solutions to producer-scrounger games. *Behavioral Ecology*, 21(2):343–348.

Mottley, K. and Giraldeau, L.-A. (2000). Experimental evidence that group foragers can converge on predicted producer-scrounger equilibria. *Animal Behaviour*, 60:341–350.

R Development Core Team (2007). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna, Austria.

Rohwer, S. and Ewald, P. W. (1981). The cost of dominance and advantage of subordination in a badge signaling system. *Evolution*, 35(3):441–454.

Steele, W. K. and Hockey, P. A. R. (1995). Factors influencing rate and success of intraspecific kleptoparasitism among Kelp gull (*Larus dominicanus*). *The Auk*, 112(4):847–859.

Stephens, D. W. (1981). The logic of risk sensitive foraging preferences. *Animal Behaviour*, 29(2):628–629.

Turner, M. G. (1989). Landscape ecology: the effect of pattern on process. *Annual Review of Ecology and Systematics*, 20:171–197.

Winterhalder, B. (1996a). A marginal model of tolerated theft. *Ethology and Sociobiology*, 17:37–53.

Winterhalder, B. (1996b). Social foraging and the behavioral ecology of intragroup resource transfers. *Evolutionary Anthropology*, 5(2):46–57.

Winterhalder, B. (1997). Gifts given, gifts taken: the behavioral ecology of nonmarket, intragroup exchange. *Journal of Archaeological Research*, 5(2):121–168.

Zann, R. A. (1996). *The zebra finch: A synthesis of field and laboratory studies*. Oxford Ornithology Series. Oxford University Press, Oxford.

CHAPTER VII

GENERAL CONCLUSION

The producer-scrounger game is one of the best studied models of social foraging, and as discussed in the introduction (section I.5), this thesis has focused on three underlying themes: contributions to the advancement of producer-scrounger models, information use in producer-scrounger games, and spatial effects on these models. In this conclusion, I will summarize and synthesize the association of the four chapters I have presented to these themes and suggest directions for future research, both theoretical and empirical.

VII.1 Summary and Synthesis

VII.1.1 Advancing the models

There are a number of basic producer-scrounger models currently in use (e.g. Vickery et al. 1991; Caraco and Giraldeau 1991; Ranta et al. 1996; Barta and Giraldeau 1998), and while the study of these models has by no means stood still (Dubois et al. 2010; Mathot and Giraldeau 2010), there remains an abundance of unanswered questions and ample space for exploration.

In Chapter II, I extended work by Beauchamp (2000) exploring learning mechanisms for foragers playing a producer-scrounger game in a spatially-explicit world. I discovered that when candidate rules such as the Relative Payoff Sum, Perfect Memory, and the Linear Operator were placed in competition using a genetic algorithm approach, population dynamics (as a function of group size) clearly favoured the Relative Payoff Sum. This result provided evidence in favour of earlier work on ES learning rules that suggested that the Relative Payoff Sum was evolutionarily stable

(Harley 1981; Tracy and Seaman Jr. 1995). The genetic algorithm also produced a previously unseen pattern in the evolution of the parameter values to the RPS which showed that specialization in tactic use increases along with group size and grid size. Our findings on environmental variation and behavioural flexibility in the producer-scrounger game provide an interesting contrast to the work of optimal foraging theorists, and pointed to different pressures on learning mechanisms operating on social foragers.

Chapter III showed that by broadening the scope of producer-scrounger relationships to include coevolutionary dynamics between predator and prey, interesting new effects of manipulative information use could be seen. Increased prey clumping forced increased use of social information by predators (increased levels of scrounging), reducing predator search efficiency and boosting prey survival. When both prey and predators were allowed to co-evolve, though, prey evolving the highest level of clumping against predators not using social information. The interpretation of these results - that prey evolved to turn predator information use against predators themselves - is a novel outcome for the producer-scrounger dynamic.

Chapter IV presents the first attempt I know of to link the evolution of a polymorphism linking the producer-scrounger to an animal personality trait such as boldness. Though there was no evidence of the expected within-population polymorphism of bold producers and shy scroungers, a strong effect of environmental parameters such as patch density and richness and predation pressure was found on overall population dynamics; bold producers evolved when faced with dense, poor patches while shy scroungers emerged when patches were sparse but rich, and predation moderated these effects. Animal personality is an area of immense focus in current behavioural ecology research, and the work in Chapter IV makes the producer-scrounger paradigm a relevant part of that focus.

Chapter V explores a cellular automata that furnishes us with a simple model to study the interaction of producing and scrounging with local, social learning effects. I discovered that the rule of thumb we used allowed for behavioural flexibility and complex population dynamics from the simplest producer-scrounger model (compare this to Dubois et al. 2010), and the effect of effective group sizes on population outcomes is an important glimpse into how real populations might organize themselves. This model also represents the simplest spatial producer-scrounger model that I am aware of.

Finally, Chapter VI demonstrates that the method of representing the landscapes upon which foragers interact can have a significant impact; I discovered that ESS values and flock geometry showed (sometimes dramatic) changes as a function of the underlying geometry, and I used this to make an argument about the ecological validity of current empirical and simulation work on this social foraging game. The producer-scrounger game is a model of exploitative behaviour that extends far beyond birds on an aviary grid; wider non-human and human animal questions of foraging, mating, and resource transfer in general (Giraldeau and Dubois 2008) will be affected by the issues raised in this chapter and my thesis in general.

VII.1.2 Information use

The producer-scrounger game is, fundamentally, a game about information use in its various forms, and the chapters of my thesis explore this aspect to the models in depth. Exploration of the use of learning rules as mechanisms for personal information gathering led to an elaboration of our understanding of the conditions under which social foragers will favour personal information use or reject it in favour of specialization and fixed strategies; the results I present suggest that group size will be an important determinant of information use in social foraging, a fact with implications for empirical work which is typically done with small group sizes (Giraldeau and Dubois 2008).

Social information is the explicit topic of Chapters III and V. Here, social information was found to be an important point of contention in the arms-race between prey and predators when allowed to co-evolve (Chapter III), and learning socially with a simple rule of thumb in a local neighbourhood was shown to provide a method of regulating population dynamics that came with great complexity and power.

Even Chapter IV contains an implicit (and powerful) effect of information use. The personality trait boldness, when coupled with the producer and scrounger tactics, responded to environmental conditions by evolving more (shy scroungers) or less (bold producers) attention to social information. In fact, it could be argued that populations composed of bold producers represents a complete breakdown of the producer-scrounger system, and raises questions for the interplay between personality and the maintenance of social foraging dynamics.

The results presented in all four chapters imply the need for integrative work to examine the shifting and possibly conflicting demands and gifts of each source of information on foraging individuals, a problem I will return to in section VII.2.

VII.1.3 Spatial social foraging

It can hardly be said that spatial effects have been ignored in behavioural ecology (e.g. Lima and Zollner 1996), but with some notable exceptions (Ruxton 1995; Barta et al. 1997; Flynn and Giraldeau 2001; Beauchamp 2008) the issue has received less attention in relation to social foraging. Spatial effects, both in terms of resource distribution and relationships among foragers, were an important component in each producer-scrounger model I developed for this thesis. The work in Chapter II demonstrated that specialization in tactic use may be related to group size (which was itself a function of grid size), and Chapter III showed that prey evolved their spatial distribution to manipulate their predators' behaviour. Scrounging in the model in Chapter IV was directly related to patch density (echoing past results such as Ruxton 1995; Beauchamp and Giraldeau 1997, which show that sparse patches reduce scrounging) and boldness as I modelled it is an inherently spatial trait, as bold individuals move away from the group and shy individuals stay close to it. Boldness and other personality traits may allow natural selection to adapt individual responses to conditions imposed not only by the physical spatial environment but also the social spatial environment, and the social spatial environment is the subject of Chapter V, where increasing effective group sizes had a strong effect on the sustainability of social foraging outcomes.

The purest example of a spatial effect arises in Chapter VI, where I showed that the way in which we represent patches (or other resources) in space, the landscape geometry, has significant effects on the predictions of the producer-scrounger model. The producer-scrounger game is studied largely in restricted aviary situations with small populations of birds on regular, square grids, and theoretical work (in the form of simulations) adopts the same landscape assumptions. In this light, the transfer of the body of producer-scrounger knowledge - to both realistic foraging situations across a variety of species and to broader questions where the game serves as a model of exploitative behaviour in general - is in question.

VII.2 Future research

The chapters of my thesis have raised as many questions as they have answered, a situation which I find eminently enjoyable. In this last section, I put forth my thoughts on the directions that future work might take.

VII.2.1 Thoughts on models

The producer-scrounger game is a simple game, but that simplicity is deceptive; there remain many avenues for elaboration and exploration. In Chapters II and V, f I investigated learning rules and rules of thumb as mechanisms for learning and information use, and there is much to be done. Empirically, both chapters provide the chance for simple and informative tests to be carried out. For example, the discussion in Chapter II pointed out that the optimal rule evolved in many cases featured a large residual for producing, suggesting that reducing producer tactic use should be difficult even if the payoff to producing is dramatically diminished. The results from that chapter also suggest that specialization should depend on group size; creating flocks large enough to distinguish this effect might be difficult in laboratory work, but if it can be achieved (or studied in field work) the model makes clear predictions about foraging behaviour.

Theoretically, work is ongoing regarding the structure of optimal learning rules. The results in Chapter II extend those found in Beauchamp (2000), but that and previous efforts have focused on a small set of arbitrary rules culled from the existing literature. By using higher-order techniques in evolutionary computation such as genetic programming, the space of possible rules can explored for even better candidate rules, which can then be tested in the same way as I have done in this thesis, and then matched to empirical observations of learning to determine fit.

The work in Chapters II and V meet in the words of McNamara and Houston (2009), who said:

> However, the world is not as simple as this or any other model. The number of situations is too vast to expect the optimal decision for every situation to evolve. Instead, it is likely that animals will evolve rules that perform well on average in their natural environment. These rules might be simple and might not be exactly optimal in any situation [...] (p.671).

As Chapter V shows, simple rules can generate complex patterns of behaviour and intricate population dynamics, and work by others has shown that complex rules may not out-perform simple rules in social foraging tasks (e.g. Arbilly et al. 2010). Thus, it would seem that the search for simple mechanisms underlying behaviour in social foraging will be a fruitful area of future exploration. Further, extending the spatial structure of the models in both Chapters V and VI to model more realistic situations (whether space is represented as geometry or social relationships) can only be of benefit to the field of social foraging. There is also a creative tension between the results of Chapter IV, wherein a personality variable drives the spatial arrangement of foragers, and Chapter VI, in which the spatial arrangement of foragers changes as a function of landscape geometry with no other mechanism required; exploring the role of mechanisms such as learning and personality in the maintenance of behavioural dynamics will require remembering that simpler mechanisms - or even a complete lack of such - may have as much explanatory power as more complicated explanations.

The study in Chapter III is another starting point for future work in the producer-scrounger family of models. The coevolution of predator-prey dynamics presented in this paper might easily be extended to account for additional traits, or made more specific by focusing on specific pairs (or groups!) of species. For instance, the prey in the model are likely to be represented best by plants or other non-moving or slow-moving prey (e.g. Avgar et al. 2008), but extending the model to allow the same coevolution with moving prey should be achievable; this could represent, as an example, lions hunting wildebeest or zebra (Scheel and Packer 1991; Barnard 1984). Another example in this vein is the evolution of dispersal in predator-prey systems (Taylor 1990); adding a dispersal mechanism into the model I present in Chapter III would be an interesting modification. The potential of this modelling methodology to explore such complicated coevolutionary questions is exciting.

Chapter IV sought to find a within-population dimorphism in personality and social foraging (bold producers and shy scroungers) that it proved impossible to locate; the question is, 'why'? Future work on this needs to bridge the gap between the empirical observations on social foraging geese that show this relationship (Kurvers et al. 2010) and theoretical work showing that negative frequency-dependent selection is a suitable mechanism to drive the evolution of animal personality (Wolf et al. 2007; Wolf and Weissing 2011). Environmental variation is often proposed as an important force in the evolution of learning (Stephens 1987; Shettleworth et al. 1988; Stephens 1991), and though informal tests (unpublished data) of our model did not find such an effect a more thorough investigation should be done.

VII.2.2 Integrating information use

Much empirical work has been done on information use in behavioural ecology (Galef and Giraldeau 2001; Danchin et al. 2004), but producer-scrounger models have not made similar strides, and I believe that future work can progress from the studies presented in this thesis. For example, tension between personal and social sources of information can lead to problems such as 'informational cascades' (Giraldeau et al. 2002; Rieucau and Giraldeau 2011), in which (incorrect) socially acquired information overwhelms personal information and results in a sub-optimal decision. Learning rules and rules of thumb, exploring the use of personal and social information, provide a rich area to model such phenomena in a social foraging context and determine the characteristics of an interface between sources of information.

VII.2.3 Foraging ahead, spatially

I believe that spatial structure will have an important part to play in future work on producer-scrounger modelling, both in the relationships between foragers and in the structure of the landscape. Between foragers, Barta et al. (1997) was among the first to point out the possibilities of spatial relationships within flocks of producers and scroungers, and Beauchamp (2008) studied the effects of spatial structure explicitly. In Chapter V, I used a cellular automata to create a simpler spatial model which I believe could form the basis for some of the future work in this area; for example, probabilistic updating rules could be used, or the effect of different neighbourhood types might be investigated. Empirical work on this question will also be important, but it will be necessary to use new species or modify current experimental designs to study larger groups and more varied spatial environments than is currently used in the majority of published work.

The results of Chapters II and V both suggest an effect of increasing group size (effective or absolute) and their interaction should be tested: does increasing specialization at larger group sizes lead to a break down of social foraging behaviour in the same ways that large effect group sizes did in the social learning model? If so, this would provide an important point of contact between the social learning and learning rules models that could help bridge the two.

In regards to landscape dynamics, further work investigating the performance of producer-scrounger models in more realistic landscapes will be important, and adding in factors such as spatial autocorrelation (Valcu and Kempanaers 2010) will greatly enhance the realism of the models. By way of illustration, we can imagine spatial autocorrelation in patch distribution (clumping) and ask how this would affect the outcome of individual-based models such as those I have used in this thesis. Integration with real landscapes as modelled with GIS (geographical information system) data would also be an exciting area of development for spatial social foraging models (Lima and Zollner 1996).

VII.3 Conclusion

The producer-scrounger game has been studied deeply (Giraldeau and Livoreil 1998; Giraldeau and Dubois 2008), but the possibilities for new research seem endless. In this thesis, I have presented research that stands as my attempt to contribute to the realization of a small fraction those possibilities, focusing largely on the themes of information use and spatial structure. Along the way I have investigated the potential of learning mechanisms and rules of thumb in social foraging, connected the personality trait of boldness to producing and scrounging, and explored the co-evolution of predators and prey information dynamics. In the final estimation, I believe that the findings of this work may have a significant effect on the evolution of producer-scrounger theory and empirical work for time to come.

VII.4 Bibliography

Arbilly, M., Motro, U., Feldman, M. W., and Lotem, A. (2010). Co-evolution of learning complexity and social foraging strategies. *Journal of Theoretical Biology*, 267(4):573–581.

Avgar, T., Giladi, I., and Nathan, R. (2008). Linking traits of foraging animals to spatial patterns of plants: social and solitary ants generate opposing patterns of surviving seeds. *Ecology Letters*, 11:224–234.

Barnard, C. J. (1984). *Producers and scroungers : Strategies of exploitation and parasitism.* Chapman & Hall, London.

Barta, Z., Flynn, R., and Giraldeau, L.-A. (1997). Geometry for a selfish foraging group: a genetic algorithm approach. *Proceedings of the Royal Society of London. Series B, Biological Sciences*, 264:1233–1238.

Barta, Z. and Giraldeau, L.-A. (1998). The effect of dominance hierarchy on the use of alternative foraging tactics: a phenotype-limited producing-scrounging game. *Behavioural Ecology and Sociobiology*, 42:217–223.

Beauchamp, G. (2000). Learning rules for social foragers: Implications for the producer-scrounger game and ideal free distribution theory. *Journal of Theoretical Biology*, 207:21–35.

Beauchamp, G. (2008). A spatial model of producing and scrounging. *Animal Behaviour*, 76:1935–1942.

Beauchamp, G. and Giraldeau, L.-A. (1997). Patch exploitation in a producer-scrounger system: test of a hypothesis using flocks of spice finches (*Lonchura punctulata*). *Behavioural Ecology*, 8:54–59.

Caraco, T. and Giraldeau, L.-A. (1991). Social foraging: Producing and scrounging in a stochastic environment. *Journal of Theoretical Biology*, 153:559–583.

Danchin, É., Giraldeau, L.-A., Valone, T. J., and Wagner, R. H. (2004). Public information: from nosy neighbors to cultural evolution. *Science*, 305:487–491.

Dubois, F., Morand-Ferron, J., and Giraldeau, L.-A. (2010). Learning in a game context: strategy choice by some keeps learning from evolving in others. *Proceedings of the Royal Society of London. Series B, Biological Sciences*, 277:3609–3616.

Flynn, R. and Giraldeau, L.-A. (2001). Producer-scrounger games in a spatially explicit world: Tactic use influences flock geometry of spice finches. *Ethology*, 107:249–257.

Galef, B. G. and Giraldeau, L.-A. (2001). Social influences on foraging in vertebrates: causal mechanisms and adaptive functions. *Animal Behaviour*, 61:3–15.

Giraldeau, L.-A. and Dubois, F. (2008). Social foraging and the study of exploitative behaviour. In Brockmann, H. J., Snowdon, C. T., Roger, T. J., Naquib, M., and Wynne-Edwards, K. E., editors, *Advances in the study of behavior*, volume 38, pages 59–104. Elsevier.

Giraldeau, L.-A. and Livoreil, B. (1998). Game theory and social foraging. In Dugatkin, L. A. and Reeve, H. K., editors, *Game theory and animal behaviour.*, pages 16–37. Oxford University Press, New York.

Giraldeau, L.-A., Valone, T. J., and Templeton, J. J. (2002). Potential disadvantages of using socially acquired information. *Philosophical Transactions of the Royal Society, Biological Sciences*, 357:1559–1566.

Harley, C. B. (1981). Learning the evolutionarily stable strategy. *Journal of Theoretical Biology*, 89:611–633.

Kurvers, R. H., Prins, H. H., van Wieren, S. E., van Oers, K., Nolet, B. A., and Ydenberg, R. C. (2010). The effect of personality on social foraging: shy barnacle geese scrounge more. *Proceedings of the Royal Society of London. Series B, Biological Sciences*, 277(1681):601–608.

Lima, S. L. and Zollner, P. A. (1996). Towards a behavioral ecology of ecological landscapes. *Trends in Ecology & Evolution*, 11(3):131–135.

Mathot, K. J. and Giraldeau, L.-A. (2010). Within-group relatedness can lead to higher levels of exploitation: a model and empirical test. *Behavioural Ecology*, 21(4):843–850.

McNamara, J. M. and Houston, A. I. (2009). Integrating function and mechanism. *Trends in Ecology & Evolution*, 24(12):670–675.

Ranta, E., Peuhkuri, N., Laurila, A., Rita, H., and Metacalfe, N. B. (1996). Producers, scroungers, and foraging group structure. *Animal Behaviour*, 51:171–175.

Rieucau, G. and Giraldeau, L.-A. (2011). Exploring the costs and benefits of social information use: an appraisal of current experimental evidence. *Philosophical Transactions of the Royal Society, Biological Sciences*, 366(1567):949–957.

Ruxton, G. D. (1995). Foraging in flocks: non-spatial models may neglect important costs. *Ecological Modelling*, 82:277–285.

Scheel, D. and Packer, C. (1991). Group hunting behaviour of lions: a search for cooperation. *Animal Behaviour*, 41:697–709.

Shettleworth, S. J., Krebs, J. R., Stephens, D. W., and Gibbon, J. (1988). Tracking a fluctuating environment: A study of sampling. *Animal Behavior*, 36:87–105.

Stephens, D. W. (1987). On economically tracking a variable environment. *Theoretical Population Biology*, 32:15–25.

Stephens, D. W. (1991). Change, regularity, and value in the evolution of animal learning. *Behavioral Ecology*, 2(1):77–89.

Taylor, A. D. (1990). Metapopulations, dispersal, and predator-prey dynamics: an overview. *Ecology*, 71(2):429–433.

Tracy, N. D. and Seaman Jr., J. W. (1995). Properties of evolutionarily stable learning rules. *Journal of Theoretical Biology*, 177:193–198.

Valcu, M. and Kempanaers, B. (2010). Spatial autocorrelation: an overlooked concept in behavioral ecology. *Behavioral Ecology*, 21(5):902–905.

Vickery, W. L., Giraldeau, L.-A., Templeton, J. J., Kramer, D. L., and Chapman, C. A. (1991). Producers, scroungers, and group foraging. *The American Naturalist*, 137(6):847–863.

Wolf, M., van Doorn, G. S., Leimar, O., and Weissing, F. J. (2007). Life-history tradeoffs favour the evolution of animal personalities. *Nature*, 447(581-585).

Wolf, M. and Weissing, F. J. (2011). An explanatory framework for adaptive personality differences. *Philosophical Transactions of the Royal Society, Biological Sciences,* 365:3959–3968.