Numéro d'ordre : xxxx 2010

Thesis

submitted in partial fulfilment of the requirements for the degree of

Doctor of Philosophy

in the discipline of

Évolution Écosystèmes Microbiologie Modélisation

UNIVERSITÉ CLAUDE BERNARD — LYON I

&

Ecología Terrestre

UNIVERSITAT AUTÓNOMA DE BARCELONA

by

Louise VAN OUDENHOVE DE SAINT GÉRY

TRADE-OFFS AND FORAGING ACTIVITY IN MEDITERANNEAN ANT COMMUNITIES

Thesis examination panel:

Jean-Louis DENEUBOURG	Professeur, Université Libre de Bruxelles	*Président du Jury*
Fred ADLER	Professeur, University of Utah	*Rapporteur*
Vincent FOURCASSIÉ	CR-CNRS, CRCA	*Rapporteur*
Alberto TINAUT	Professeur, Universidad de Granada	*Rapporteur*
Carlos BERNSTEIN	DR-CNRS Émérite, LBBE	*Directeur de thèse*
Xim CERDÁ	CR-CSIC, Estación Biológica de Doñana	*Directeur de thèse*
Alain LENOIR	Professeur Émérite, Université de Tours	*Examinateur*
Anselm RODRIGO	Professeur, Universitát Autónoma de Barcelona	*Examinateur*

Anticipated date of defense: December 17, 2010

Résumé

Une question fondamentale en Écologie des Communautés est la compréhension des mécanismes permettant la coexistence des espèces. Dans les communautés de fourmis, le rôle de la compétition inter-spécifique est prépondérant. Certaines espèces dites comportementalement dominantes monopolisent les ressources, privant ainsi les espèces dites comportementalement subordonnées. La coexistence des espèces dominantes et subordonnées repose sur des compromis évolutifs concernant les capacités compétitives. Dans les communautés de fourmis méditerranéennes, les capacités compétitives des espèces sont liées à leurs stratégies d'approvisionnement. Les espèces les plus dominantes font généralement preuve d'un plus grand degré de communication pour collecter la nourriture. Cette thèse étudie comment les stratégies d'approvisionnement contribuent aux compromis évolutifs et articulent la diversité des communautés de fourmis.

La première partie s'intéresse au rôle des stratégies d'approvisionnement dans l'alternative entre découvrir vite les ressources et être capable de les soustraire au contrôle des compétiteurs. Ce compromis entre la découverte et le contrôle des ressources se base sur une répartition des ouvrières de la colonie entre celles qui recherchent la nourriture, et celles qui l'exploitent et la défendent. Les modèles mathématiques proposés sont développés à l'échelle évolutive et démontrent que ce principe simple peut expliquer la diversification des stratégies d'approvisionnement. La structure théorique proposée peut être élargie et servir de base conceptuelle à l'étude de la dynamique évolutive de traits d'histoire de vie chez les insectes eusociaux.

La seconde partie est centrée sur le compromis évolutif entre la dominance comportementale et la tolérance thermique. Les espèces dominantes sont généralement plus sensibles aux températures stressantes, i.e. élevées dans les communautés méditerranéennes. L'hypothèse sous-jacente concerne le rôle de la phéromone dans la communication chez les fourmis. Les composés chimiques étant détériorés par les températures élevées, l'avantage présenté par des stratégies d'approvisionnement reposant sur la communication chimique peut être nuancé. Dans les écosystèmes méditerranéens soumis à des importantes variations de température à la fois saisonnières et journalières, la diversité des stratégies d'approvisionnement contribue ainsi à la diversité des communautés de fourmis.

Resumen

Una cuestión fundamental en la Ecología de Comunidades es comprender los mecanismos que permiten la coexistencia de las especies. En las comunidades de hormigas, el papel de la competencia interespecifica es preponderante. Algunas especies, llamadas dominantes comportamentales, monopolizan los recursos, privando así las especies llamadas subordinadas comportamentales del acceso al recurso. La coexistencia de especies dominantes y subordinadas está basada en unos compromisos evolutivos referidos a las capacidades competitivas. En las comunidades mediterráneas de hormigas, las capacidades competitivas de las especies están vinculadas a sus estrategias de aprovisionamiento. Las especies más dominantes usan, generalmente, un grado más elevado de comunicación para la recolección del alimento. Esta tesis estudia cómo las estrategias de aprovisionamiento contribuyen a los compromisos evolutivos y articulan la diversidad de las comunidades de hormigas.

La primera parte está enfocada a estudiar el papel de las estrategias de aprovisionamiento frente a la alternativa entre descubrir rápidamentente los recursos o ser capaz de expulsar a los competidores de los mismos. Este compromiso entre el descubrimiento y el control de los recursos está basado en una repartición de las obreras de la colonia entre las exploradoras que buscan la comida y las reclutadas que explotan y defienden los recursos. Los modelos matemáticos propuestos están desarollados a una escala evolutiva y demuestran que este principio simple puede explicar la diversidad de las estrategias de aprovisionamiento. La estructura teórica propuesta puede extenderse y servir de base conceptual para el estudio de la dinámica evolutiva de los caracteres de estrategias vitales (life-history traits) en los insectos sociales.

La segunda parte se centra sobre el compromiso evolutivo entre la dominancia comportamental y la tolerancia térmica. Las especies dominantes son, generalmente, más sensibles a las temperaturas estresantes, i.e. elevadas en las comunidades mediterráneas. La hipótesis subyacente concierne al papel de la feromona en la comunicación entre las hormigas. Los compuestos químicos se deterioran por las temperaturas altas, y la ventaja presentada por las estrategias de aprovisionamiento basadas en la comunicación química puede resultar atenuada. En los ecosistemas mediterráneos, sometidos a variaciones de temperaturas importantes, tanto estacionales como diarias, la diversidad de las estrategias de aprovisionamiento contribuye así a la diversidad de las comunidades de hormigas.

Agrade—ciements

Agradezco a mis directores Carlos Bernstein y Xim Cerdá por su confiancia. Gracias a vos, Carlos, por enseñarme la rigor cientifica. Te agradezco también por impedir que el acento andalú haya sido convergence stable ! Gracias a tí, Xim, por estar siempre disponible para resolver mis dudas hormigueras, aguantar mis dudas existenciales, trabajar en el campo, o tomar cervecitas.

Je remercie les membres de mon comité de pilotage: Franck Courchamp, Claire Detrain, Dominique Fresneau, et Minus van Baalen.

Agradezco a Raphaël Boulay por su ayuda inconmensurable con la parte experimental, sus buenas ideas, sus críticas constructivas, y su disponibilidad.

Je remercie infiniment Alain Lenoir de m'avoir initiée à la chromatographie, et d'avoir partagé ses connaissances avec tant d'enthousiasme et de patience.

Je remercie Élise Billoir pour l'initiation à l'inférence Bayésienne et pour son amitié.

Agradezco a los colegas de la Estación Biológica de Doñana. Gracias a todo el equipo hormiga. Merci infiniment à Camille et Jessica, y gracias a Ana, Michael, Fernando, Ángel, Elena y Stéphane. Gracias a los de la comuna : Alicia, Amparo, Ana, et al. Agradezco tambien a los que hacen de la EBD un edificio vivo: los vigilantes, las limpiadoras que cantan flamenquito... y los de mantenimiento que me ayudaron a cortar cientos de palos !

Je remercie les membres du laboratoire de Biométrie et Biologie Évolutive. Je remercie particulièrement Perrine et Thibaut. Merci aussi à Manu, Isa, et à toute l'équipe Écologie Comportementale. Merci à Laurent Gueguen pour son aide en maths. Merci à Sophie, Simon, Patricia, Alex, les filles de la chorale, les grimpeurs, et les capoeiristes. Merci enfin à Nathalie,

aux gentils informaticiens, et à tous ceux qui participent à la vie du labo.

Je remercie ma comparse Lucie Froissart, ainsi que les autres camarades du SERL 2009 pour cette expérience... enrichissante ? Merci à Sophie L., Julien, Étienne, Pierre, Vincent F., Vincent T., Manue, Maud, Alexis, Gwenaël, Gilles, Agnès , Christina, et Hughes.

I thank all the collegues I had the pleasure to meet in scientific meetings. I am particularly grateful to Claus Rueffler for pertinent critics of chapter 3. I thank Hans Metz for introducing me to the evolutionary isoclines. I thank Don Feener for being so confident in the interest of my work.

Je remercie les collègues d'Antibes qui, au tout début de ma thèse, m'ont initiée à la théorie du contrôle. Merci à Frédéric Grognard, Ludovic Mailleret, et Andrei Akhmetzhanov.

Agradezco a Javier Retana por ser mi tutor en la UAB. Gracias a Xim Cerdá junior por las matriculas en la UAB.

Je remercie Hédi Soula ainsi que Sandrine et Hubert Charles pour m'avoir permis d'enseigner au cours de ma thèse.

Je remercie mon frère Georges, qui s'appelle Thomas, et qui murmurre à l'oreille des pingouins. Merci pour la mise en page LaTeX.

Je remercie très très fort mes parents et toute ma famille pour leur soutien inconditionnel. Gràcies a tot-hom.

Je remercie $\mathcal{E}$lise, Léa, Thierry, Deborah, Thibaud y todos los tangueros.

Ringrazio Anna, Luca y Lunita.

Agradezco Fernando Amor por sus photos espectaculares.

Je remercie Hélène Lagnieu pour ses aquarelles.

I thank my dad for his help. Merci papu !

Contents

List of Figures

List of Tables

Introduction

CHAPTER 1

General introduction

1.1 Ants: Eusociality & Communication

1.1.1 Eusociality & Fitness measures

More than 12,500 ant species are currently identified over the world (Agosti and Johnson, 2005). All these species present many differences both at the morphological and behavioural levels. Nevertheless, they share a very particular characteristic: all of them display the highest level of social organisation, *eusociality*. According to Wilson's definition (1971), the concept of eusociality involves three features: overlapping of generations, cooperative brood care, and reproductive division of labour. The origin of eusociality, especially regarding the existence of non-reproductive workers, has been extensively studied (Hölldobler and Wilson, 1990; Crozier and Pamilo, 1996) and is still under discussion nowadays (Nowak et al., 2010).

When Darwin (1859) wrote *On the Origin of Species* 151 years ago, he first considered the sterile workers of eusocial insect colonies as a threat for his whole theory: "I allude to the neuters or sterile females in insect-communities: for these neuters often differ widely in instinct and in structure from both the males and fertile females, and yet, from being sterile, they cannot propagate their kind [...] how is it possible to reconcile this case with the theory of natural selection?". Further, he suggested that "selection may be applied to the family, as well as to the individual". Progress in genetics exploited Darwin's intuition by theorising that selection acts at the gene level (Dawkins, 1976). This perspective led to the theory of *Kin selection* that argues that genes can spread by increasing both the fitness of its bearer (direct fitness) and the fitness of relatives sharing copies of the gene (indirect fitness) (Hamilton, 1964a,b).

Kin selection theory is based on the concept of *inclusive fitness* (Hamilton, 1964a). Contrary to the classical Darwinian fitness that considers the direct contribution of individuals (Eq. 1.1), inclusive fitness concept also takes into account the number of offspring produced by relatives (Eq. 1.2). Direct fitness ($\mathbb{F}_D$) could be defined as the number of adult offspring produced by an individual i ($n_{\text{off}}(i)$) relatively to the average production of the population ($\bar{n_{\text{off}}}$):

$$\mathbb{F}_D(i) = \frac{n_{\text{off}}(i)}{\bar{n_{\text{off}}}} \tag{1.1}$$

Inclusive fitness $\mathbb{IF}$ also integrates the direct fitness of the collateral relatives $n_{\text{off}}(j)$ according to the degree of relatedness $b(i,j)$, that might be considered as the probability of sharing a same allele:

$$\mathbb{IF}(i) = \frac{n_{\text{off}}(i) + \sum_j n_{\text{off}}(j) b(i,j)}{\bar{\mathbb{IF}}} \tag{1.2}$$

Maximising such a measure of fitness, kin selection formalises that altruistic behaviour might spread into a population depending on the degree of relatedness between individuals (Hamilton's rule).

Sterile workers are altruistic since they deny their own reproduction and help the queen to propagate her own genes. Consequently, eusocial insect societies constitute a good model to test Hamilton's theory. If genetic relatedness among social insect colonies (Crozier and Pamilo, 1996) bears out kin selection theory, the most striking support comes from the combination of kin selection with Fisher's sex-ratio theory (1930). Indeed, haplodiploidy generates peculiar relatedness patterns. In haplodiploid organisms, such as Hymenoptera, diploid females develop from fertilised eggs whereas haploid males develop from unfertilised eggs. Haplodiploidy produces thereby closer relatedness among daughters: sisters are related by 0.75 while brother-brother and brother-sister relatedness is 0.25. This relatedness asymmetry generates worker-queen conflicts about the ratio of investment (Trivers and Hare, 1976). Queens prefer sex-ratio equilibrium whereas workers have advantage in female-biased sex-ratio. Many studies in colonies of ants, wasps and bees provided evidence for sex-ratio differences based on relatedness (Trivers and Hare, 1976; Hölldobler and Wilson, 1990; Queller and Strassmann, 1998).

Inclusive fitness theory has inspired many theoretical models of social insect societies. Individual-level selection enlightens the conflicts underpinning social Hymenoptera colonies. Conflicts over sex allocation (male or female), reproductive allocation (queen or worker), and male parentage (queen's or workers') were identified and their influence on colony structure has been emphasised (Bulmer and Taylor, 1981; Bulmer, 1981; Boomsma and Grafen, 1991; Pamilo, 1991; Ratnieks and Reeve, 1992; Crozier and Pamilo, 1996; Bourke and Ratnieks, 1999; Bourke and Chan, 1999; Reuter and Keller, 2001; Ohtsuki and Tsuji, 2009). The raising of genotypic diversity by polygyny (several reproductive queens per colony) or polyandry (several mating males per queen) might also influence the strength of these conflicts (Pamilo, 1991). Reuter and Keller's model constitutes an excellent example of kin selection models since these authors propose a simple framework adapted to a colony divided into three castes: males, gynes (reproductive females), and workers (Eq. 1.3). They consider two kinds of investment: f represents the proportion of resource allocated to females, and w the part of the previous investment allocated to workers production. F and M designate the population means of the same features. Reuter and Keller (2001) suggest that the inclusive fitness $\mathbb{F}_R(X)$ of a colony member X depends on the return productivity function $b(f, w)$, the relatedness with females g_{fX} (resp. males g_{mX}) and the reproductive value of females ν_f (resp. males ν_m) as follows:

$$\mathbb{F}_R(X) = b(f,w)[\frac{f(1-w)g_{fX}\nu_f}{F(1-W)} + \frac{(1-f)g_{mX}\nu_m}{(1-F)}] \tag{1.3}$$

This kind of model is particularly suitable when focusing on investment conflicts within the colony (Beekman et al., 2003).

Notwithstanding, the key role of kin selection in the evolution of sociality is being controverted (Queller and Strassmann, 1998; Linksvayer and Wade, 2005; Wilson and Hölldobler, 2005; Wilson, 2008; Nowak et al., 2010). Some authors noted the importance of parental manipulation and maternal care (Alexander, 1974; Michener and Brother, 1974; Wade, 2001; Linksvayer and Wade, 2005). Others argue that relatedness is not the cause, but the consequence of eusociality. They suggest that the strong binding force in eusociality evolution is group selection (Wilson and Hölldobler, 2005; Nowak, 2006; Nowak et al., 2010). Theoretical evidences suggest that altruistic behaviour is promoted when the inter-group advantage exceeds the within-group cost (Nowak, 2006; Traulsen and Nowak, 2006). Some authors consider that the key step in the evolution of eusociality would be the combination of a valuable and defensible nest (Queller and Strassmann, 1998; Nowak et al., 2010).

This colonial-level selection is particularly pertinent when considering the insect colony as an organism (Wheeler, 1911). An organism whose reproduction would be managed by the sexuals (males and fertile females) as germline cells, and whose somatic cells would be represented by the workers. However, the terminology of "superorganism" is rather controversial because of the relatedness asymmetries and the existence of conflicts between subunits (Ratnieks and Reeve, 1992; Keller and Chapuisat, 2002). Oster and Wilson (1978) conceive the colony as a "factory enclosed in a fortress". In order to maximise its Darwinian fitness, a colony might maximise its energy capital by both extracting energy from the environment and protecting its investment. This capital is then converted into colonial reproduction. This economic metaphor has been modelled by Macevicz and Oster (1976). They proposed a system of differential equations (Syst. 1.4) representing the colony demography dynamics. Resources are gathered by the workers and are invested in the production of both workers and sexuals (Fig. 1.1).

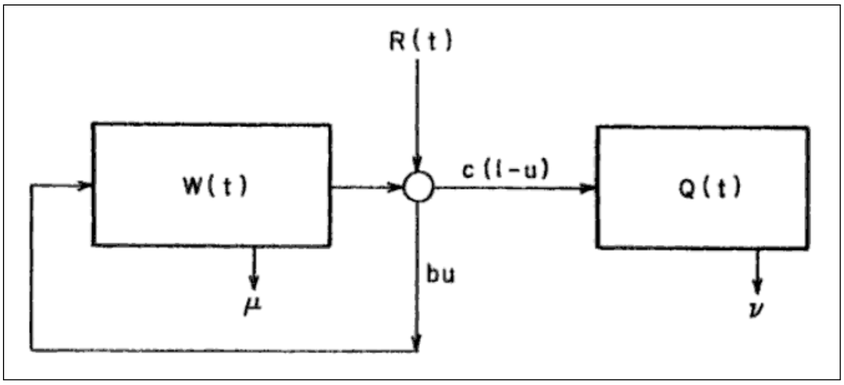


Figure 1.1 — Scheme of the demographic model of Macevicz and Oster (1976). The colony is divided into two castes: the worker population W and the reproductives Q. At any time t, workers gather resources at a per capita rate $R(t)$. A fraction $0 \leq u(t) \leq 1$ is reinvested into producing new workers, and the remaining fraction $1-u$ into reproductives. b and c respectively measure the efficiency of resources conversion into new workers and new reproductives while μ (respectively nu) stand for the per capita mortality rate of workers (resp. reproductives). (from (Oster and Wilson, 1978))

The return function $R(t)$ summarises both resource abundance and foraging efficiency of workers and represents the rate of energy gathered per worker at time t. $u(t)$ stands for the percentage of energy invested into producing new workers at a given time t. Parameters b and c respectively measure the efficiency of resource conversion into new workers and new reproductives while μ (resp. nu) stands for the per capita mortality rate of workers (resp. reproductives). $W(t)$ counts for the number of workers. The growth of the worker population within the colony depends on $W(t)$, b, $u(t)$, $R(t)$, μ, and b_1, the maximal number of workers a colony might reach (due for instance to egg limitation of the queen). $Q(t)$ is the number of sexuals produced, and depends on $(1-u(t))$, $W(t)$, $R(t)$, and ν as follows:

$$\begin{cases} \dfrac{dW(t)}{dt} = u(t)bW(t)R(t)(1-\dfrac{W(t)}{b_1}) - \mu W(t) \\ \dfrac{dQ(t)}{dt} = (1-u(t))cW(t)R(t) - \nu Q(t) \end{cases} \tag{1.4}$$

Macevicz and Oster's initial model aimed to resolve the best resource allocation schedule $u(t)$ that maximises fitness. As fitness criterion, they considered the total number of reproductives produced by the colony at the end of the colony cycle. Mathematically, they maximise the fitness function $\mathbb{F}_M$

$$\mathbb{F}_M = Q(T) \tag{1.5}$$

where T is the length of the season. They use optimal control theory, in particular the maximum principle for non-autonomous fixed time problems (Pontryagin et al., 1962) to predict a "bang-bang" strategy (a term used to denote an all-or-nothing control strategy). The allocation strategy that maximises fitness consists in an initial ergonomic phase characterised by workers production (the first "bang") followed, at the end of the season, by a reproductive phase (production of reproductives, the second "bang").

Many developments have been added to the initial model. It has been adapted to different colony structures (Oster and Wilson, 1978) including the differentiation of the reproductive caste into male and females (Bulmer, 1983). The interplay between mortality and return rate functions has been analysed to study the trade-off between foraging performance and mortality risks (Houston et al., 1988b). Experimental tests confirmed that the association colony size and sexuals production is food constrained (Sorvari and Hakkarainen, 2007). However the occurrence of the predicted bang-bang strategy in nature seems not to be a constant feature among insect colonies (Greene, 1984; Cassill, 2002). The initial model was adapted to specific situations in the following way: the assumption of egg laying dependence on foraging effort was released (Beekman et al., 1998); a "yoyo-bang" model was suggested for iteroparous societies (that reproduce repeatedly) in which colony size fluctuates with short-term nutritional deficits (Cassill, 2002); delay in larval development was modelled (Mitesser et al., 2006); high colony size loss in per capita efficiency was studied (Poitrineau et al., 2009); and discrete time models (with different rather than differential equations) were also developed (Beekman et al., 1998; Mitesser et al., 2006, 2007a,b). The heuristic power of Macevicz and Oster's model might be extended to other frameworks based on colonial-level selection either by maximising the spread of the queen's genome (Franks et al., 1990) or by modelling the colony as a hierarchically structured population (Brian et al., 1981; Al-Khafaji et al., 2009; Ohtsuki and Tsuji, 2009).

In summary, many theoretical works have already proposed different measures of fitness in eusocial insects. The notable difference between them is to focus either on the individual or on the colonial level. The use of the former kind of model might be pertinent in case of conflictual behaviour such as workers egg-laying. On the other hand, the latter kind of model might be more suitable to study synergistic behaviour such as foraging.

1.1.2 Communication & Foraging strategies

If fitness models help to identify the ultimate causes (the "whys") of specific behaviours, a better understanding of the proximate mechanisms (the "hows") is also crucial. In particular, collective motions in social insects deserve a special attention. In insect colonies, queens are nothing but egg-layers (Hölldobler and Wilson, 1990). There is no centralised authority and no global supervision of tasks. The challenge is thus to explain how those individuals whose "cerebral ganglia are not so large as the quarter of a small pin's head" (Darwin, 1871) are able to display such complex behaviours as decision making in collective foraging (Deneubourg and Goss, 1989) or chain formation to bridge a gap (Lioni and Deneubourg, 2004)? "The secret is in the intercommunication of [colonies'] members" revealed Wiener (1961). The ability to organise coordinated action without centralised control does not emerge from individual complexity, but is structured by interactions (Deneubourg and Goss, 1989; Deneubourg et al., 1990). Collective behaviours in insects might thus be considered as self-organised (Camazine et al., 2001; Bonabeau et al., 1997; Theraulaz et al., 2003; Sumpter, 2006). *Self-organisation* designates pattern-formation processes that produce complex global patterns from simple repeated local interactions (Camazine et al., 2001). In such systems, the amplification of random fluctuations is driven by positive (amplification) and negative (counterbalance) feedback. Self-organisation occurs in many behaviours performed by social insects such as nest construction (Franks and Deneubourg, 1997) or foraging (Detrain and Deneubourg, 2006). Individuals respond to task-related stimuli according to a fixed threshold (Bonabeau et al., 1996; Theraulaz et al., 1998), and collective patterns emerge from the interplay between randomness, amplification processes, and the number of individuals (Deneubourg et al., 1986). However, before developing the self-organised patterns of foraging in ants, we shall first focus on the details of this system (Gordon, 2007).

Ants use a huge variety of procedures for the discovery and retrieval of food. Foraging strategies can be classified in different categories. Classification systems vary slightly among authors (Wilson, 1971; Carroll and Janzen, 1973; Oster and Wilson, 1978; Sudd and Franks, 1987; Beckers et al., 1989; Hölldobler and Wilson, 1990). Moreover, the pertinence of some classifications is controversial due to the wide diversity of behaviours regarding foraging activity (Traniello, 1989). Notwithstanding, classifications might be useful to get a better understanding of the more significant differences between species. The very first differentiation is between recruiting and non-recruiting species. Some species forage individually. Foragers that discover a food source do not share the information with nestmates. For instance, some *Gigantiops* (Beugnon et al., 2001), *Dinoponera* (Fourcassié and Oliveira, 2002) and most of the *Cataglyphis* sp. (Lenoir et al., 1990; Ruano et al., 2000) use individual foraging. In some species though, successful foragers could be able to stimulate nestmates' foraging without communicating resource location (Amor et al., 2010). Other species do recruit. Recruitment in a foraging task might be defined as the communication process that drives nestmates to food source location (Wilson, 1971). Following Deneubourg et al.'s broad classification (1983), recruitment behaviour might be distinguished into three categories: tandem-running, group recruitment, and mass-recruitment. In tandem-running, a successful forager drives a nestmate either by direct contact (Wilson, 1959) or by individual-specific chemical trails (Jessen and Maschwitz, 1986). This kind of recruitment is common in Temnothorax sp. (Beckers et al., 1989). Since it involves bidirectional feedback between individuals, it might be considered as a teaching behaviour (Franks and Richardson, 2006). In group recruitment, a successful forager lays a trail while returning to the nest, and guides a group of nestmates to the food source. This strategy is used for instance in some *Camponotus* (Hölldobler, 1971; Kohl et al., 2001; Boulay et al., 2007a) or *Aphaenogaster* species (Cerdá et al., 2009; Lenoir et al., prep). In mass recruitment, a scout lays a chemical trail that stimulates independent trail-following and trail-laying of nestmates. This kind of recruitment is broadly used by many ant species (e.g. leaf-cutting *Atta* sp.Jaffe and Howse 1979; Roces 1994).

When ants lay a trail to recruit nestmates, they press their gaster on the ground, and release tiny droplets of pheromones. This term designates a chemical substance used in communication (Karlson and Lüscher, 1959). Unlike hormones assigned to communication within the organism, pheromones are the semiochemicals implicated in the communication between individuals of the same species. In ants, trail pheromone originates in one or more abdominal glands such as poison gland (e.g. *Tetramorium impurum* Morgan and Ollett 1987), Dufour gland (e.g. *Solenopsis invicta* Van der Meer 1983), hind gut (e.g. *Lasius fuliginosus* Huwyler et al. 1975), pygidial gland (e.g. *Tapinoma simrothii* Hefetz and Lloyd 1983), and Pavan gland (e.g. *Linepithema humile* Van Vorhis Key and Baker 1982) according to the species (see Morgan (2009) for review). Trail pheromone composition involves generally several compounds. This chemical blend is very variable between species (Appendix A). Trail pheromone attractiveness both stimulates and guides ants (Hölldobler and Wilson, 1990). Excitation and orientation functions might be assured by different signals with different longevity. In some species, the chemical communication process combines a short-lived stimulating signal with a long-lasting orientating signal (Dussutour et al., 2009; Lizon à l'Allemand and Witte, 2010). Some species might also use repellent pheromone to prevent positive feedback when necessary (Robinson et al., 2005, 2008).

In summary, the recipe to synergy in collective foraging is communication. Communication between individuals would enable to make the effective range of perception wider than the actual sensory range (Couzin, 2007). In ants, communication is mostly mediated by chemical signals, and might be combined with other sensory cues such as vibrational or tactile stimuli (Hölldobler, 1995). Ants display specific behaviours to efficiently exploit their environment. However, the study of these foraging behaviours make little sense without reference to the ecology of the species and the cornerstone of ant ecology is competition (Hölldobler and Wilson, 1990).

1.2 Ant communities

1.2.1 Competition: Concepts & Challenges

Competition might be broadly defined as fitness reducing interactions between organisms or species. Competition can be indirect via the consumption of a common limited resource (exploitation competition) or direct when interactions between individuals affect their reproduction or survival (interference competition) (Park, 1962). Spatial competitive mechanisms can be more precisely classified according to the kind of interactions involved (Schoener, 1983).

The main challenge about competition is to explain the coexistence of competitors. Indeed, according to the "competitive exclusion principle", also called Volterra-Gause principle, there cannot be more species than limiting resources (MacArthur and Levins, 1964). In nature though, a huge diversity of species can be observed (Hutchinson, 1959). To explain this diversity, Hutchinson and MacArthur (1959) introduced the concept of niche partitioning: "the properties of the niches of different species are defined by the numbers of kinds of interface between a limited number of sorts of randomly distributed environmental mosaic elements". In brief, as clearly exposed by Dr. Suess (Geisel, 1955):

> *And* NUH *is the letter I use to spell Nutches*
> *Who live in small caves, known as Nitches, for hutches.*
> *These Nutches have troubles, the biggest of which is*
> *The fact there are many more Nutches than Nitches.*
> *Each Nutch in a Nitch knows that some other Nutch*
> *Would like to move into his Nitch very much.*
> *So each Nutch in a Nitch has to watch that small Nitch*
> *Or Nutches who haven't got Nitches will snitch.*

Practically, niche differentiation is mediated by competitive trade-offs (Kneitel and Chase, 2004). These trade-offs consist in negative functional interactions between life history traits improving competitive ability on the one hand, and those enhancing population growth on the other. For instance, since the energy allocated to reproduction is limited, there is a functional trade-off between seed sizes and seed number. Bigger seeds are better competitors, but the dispersal rate increases with seed number (Geritz, 1998). This negative interaction underpins the so-called competition-colonisation trade-off predicting that species with higher dispersal rates persist in sites not occupied by superior competitors (Tilman, 1994; Calcagno et al., 2006). These kind of trade-offs between competitive ability and frequency-independent fitness component shape coexistence patterns (Adler and Mosquera, 2000).

1.2.2 Dominance hierarchy & Trade-offs

Interspecific competition structures ant communities into a linear dominance hierarchy (Fellers, 1987; Savolainen and Vepsäläinen, 1988; Hölldobler and Wilson, 1990; Palmer et al., 2000; Parr and Gibb, 2010). Andersen (1992) considers "dominance to have both numerical and functional components: that is, a dominant species is abundant and also has a strong competitive influence on other species". In agreement, Davidson (1998) defines the "ecological dominance" as a combination of "numerical dominance" (abundance in a given community) and "behavioural dominance" (superiority in interspecific encounter competition sensu Schoener 1983). Species are roughly classified into two categories: dominant and subordinate. Dominant species are aggressive and tend to exclude subordinates from resources while subordinate species generally avoid direct interactions with dominants. Nevertheless, community structure obviously depends on the ecosystem considered. Regarding the effect of dominant species for instance, Gibb and Hochuli (2004) demonstrated the limit of dominant effect on subordinate distribution in Australian communities, whereas the top dominant species actually affects all the ant species of Finnish islands (Savolainen and Vepsäläinen, 1988). The gross categorisation dominant/subordinate should thus be specified according to the focused community.

Regarding Finnish ant communities, Vepsäläinen and Pisarski (1982) and Savolainen and Vepsäläinen (1988) presented a three-level linear competition between the "territorial species" (top competitors, they defend both food and foraging area), "encounter species" (aggressive but nonterritorial, they defend food) and "submissive species" (nonagressive) (Savolainen and Vepsäläinen, 1989).

Andersen (1992, 1995) proposes a classification of Australian seasonal tropic communities based both on the phylogeny and the competitive interactions. He differentiates seven functional groups: i/ *Dominant Dolichoderinae* (DD) are abundant, highly active and aggressive. ii/ *Subordinate Camponotini* (SC) are behaviourally subordinate to the DD, but are dominant in their absence. iii/ *Climate specialists* (CS) are distributed among the arid (Hot CS), humid (Tropical CS) or cool-temperate (Cold CS) regions. iv/ *Cryptic* species are tiny and do not have competitive interaction with other ants. v/ *Opportunists* are unspecialised poor competitors abundant in disturbed areas. vi/ *Generalized Myrmicinae* are good competitors but not aggressive. vii/ *Specialist predators* are medium to large size species mainly predating other arthropods .

The challenge in such dominance hierarchies is to identify the compensatory mechanisms that allow competitively subordinate species persistence and coexistence with dominants. The first argument deals with the condition-dependence of the dominance hierarchy robustness. Interspecific interactions rely on the resource characteristics such as food quality (Sanders and Gordon, 2003), size (Cerdá et al., 1998b), and density (Stringer et al., 2007; Lester et al., 2010)), and on abiotic factors such as temperature (Cerdá et al., 1997). Species coexistence might thus be promoted by short-term variations (Palmer et al., 2000) and spatial and temporal niches partitioning (Albrecht and Gotelli, 2001). Both niche differentiation processes and coexistence patterns when niches overlap are mediated by competitive trade-offs.

The so-called *Dominance-Discovery* trade-off refers to the negative correlation between the ability to defend food sources and the ability to find them (Fellers, 1987; Perfecto, 1994; Holway, 1999; Lebrun and Feener, 2007; Adler et al., 2007). Subordinate species (also called scramblers, Savolainen and Vepsäläinen 1988; or submissive Davidson 1998) privilege fast resource finding (Pearce, 2008) and tend to avoid encounters. Conversely, dominants (also known as encounter species, Fellers 1987; contesters, Savolainen and Vepsäläinen 1988; or extirpators, Davidson 1998), are slower for resource discovery, but are able to drive other species away.

Invasive species though, are known to break this common trade-off (Fig. 1.2). The Argentine ant, for instance, is efficient at both locating and controlling baits (Holway, 1999). The hypothesis proposed by Feener (2000) considers that invasive species are actually released from a trade-off between dominance and sensibility to specific enemies, such as parasitoids. Indeed, the ability to dominate resources seems positively correlated with parasitoid vulnerability (Lebrun, 2005). This Dominance-Parasitoid Vulnerability trade-off occurs in communities where parasitoid flies attack specific host species (Feener, 2000). Moreover, specific enemy attacks reduce the host's competitive ability by indirect costs of anti-parasitoid defence behaviour (LeBrun and Feener Jr, 2002; Lebrun and Feener, 2007). Interspecific parasitoid-mediated competition generates then what Adler (1999) called the "balance of terror" between competitors and specific enemies. There is thus an interaction between trade-offs, Dominance-Discovery trade-off being reinforced by the balance of terror (Lebrun and Feener, 2007).

In some ant communities though, the Dominance-Discovery trade-off does not occur

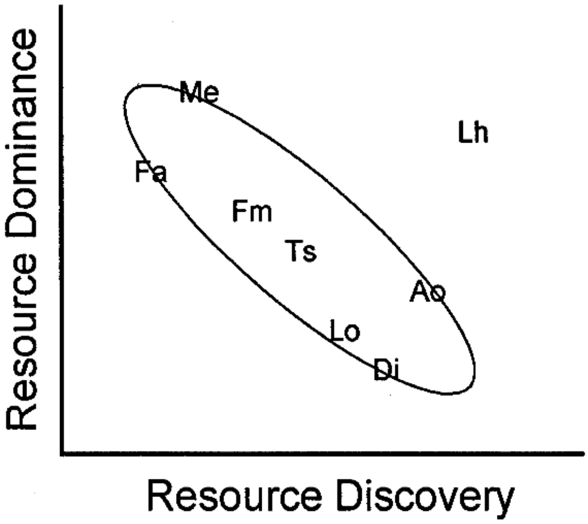


Figure 1.2 — Dominance-Discovery trade-off in a temperate woodland ant assemblage in northern California. Species ability to dominate resources was represented according to their efficiency in resource discovery. The invasive Argentine ant (Lh: *Linepithema humile*) does not follow the trade-off curve. Native species were: Ao: *Aphaenogaster occidentalis*, Di: *Dorymyrmex insanus*, Fa: *Formica aerata*, Fm: *Formica moki*, Lo: *Liometopum occidentale*, Me: *Monomorium ergatogyna*, Ts: *Tapinoma sessile*. Data are from Holway (1999) and graphical representation was proposed by Feener (2000).

(Santini et al., 2007; Lessard et al., 2009). Nevertheless, a negative correlation might be found between behavioural dominance and thermal tolerance. Subordinate species tend to be more tolerant to stressful temperatures (Bestelmeyer, 1997; Cerdá et al., 1997; Wittman et al., 2010). As a result, behavioural dominant species are most active at mild temperature while subordinate species are still active at extreme temperatures (Cerdá et al., 1998c; Bestelmeyer, 2000; Lessard et al., 2009). This Dominance-Thermal Tolerance trade-off structures coexistence patterns in environment where temperature is stressful, either low or high. In the southern Appalachians (USA) where temperature varies over the year from 3°C to 19°C, species foraging at low temperature tend to be subordinate (Lessard et al., 2009). In the Siskiyou mountains (USA), soil-surface temperature ranges from 10 °C to 75°C, and dominant species are limited by high temperatures (Wittman et al., 2010). This is also the case in Mediterranean ant communities.

1.2.3 Mediterranean ant communities

Gómez et al. (2003) attempted to use Andersen's functional groups in a Mediterranean sub-humid region (northeastern Spain). However, the adequacy of such a classification in

Mediterranean communities might be questioned. Regarding the *Dominant Dolichoderinae* for instance, Andersen (1995) wrote: "They are particularly abundant and diverse in hot and open habitats [. . .] and are often absent from heavily shaded sites". The widespread Dolichoderinae in Mediterranean communities are *L. humile* and *T. nigerrimum* (Gómez et al. (2003), see also Table 1.3). The former is an invasive species (Giraud et al., 2002), indubitably dominant (Carpintero and Reyes-López, 2008). The latter is also a behaviourally dominant species (Cerdá et al., 1997). However, both of them are limited by high temperatures, while vegetation cover increases their abundance (Cros et al., 1997; Cerdá et al., 1997; Retana and Cerdá, 2000; Holway et al., 2002; Thomas and Holway, 2005). This example clearly demonstrates that Australian and Mediterranean communities slightly mismatch.

Mediterranean ecosystems are characterised by important temperature variations both at the seasonal and daily scales. For instance, in Doñana National Park (Huelva, Spain), temperatures vary from 0°C to 20°C in January to 15°C to 45°C in July (mean data on the 1978-2007 period). In particular, in a same summer day, ground temperature fluctuate between 15°C and 55 °C (Angulo et al., *In press*). These variations interplay with the diversity of vegetation covering that ranges from open areas, grassland, shrubland, to forests. Indeed, canopy cover prevents very high ground temperatures in summer, and influences thereby ant community structure (Retana and Cerdá, 2000; Arnan et al., 2007).

As in most other ants community, species might be divided into dominants and subordinates according of their ability to drive other species away from baits. Four groups might be distinguished according to competitive interaction outcomes (Table 1.3):

- *Invasive* species were isolated because of their strong tendency to break community structuring trade-offs (Feener, 2000). The Argentine ant *L. humile* is the main invasive species in Mediterranean communities and does not display notable differences from other dominant species (Table 1.3). Other invasive species were identified. For instance, *Lasius neglectus* is locally expanded in Cataluña (Espadaler et al., 2007).

- *Dominant* species have better fighting abilities (Retana and Cerdá, 1995) and are able to chase other species away from baits.

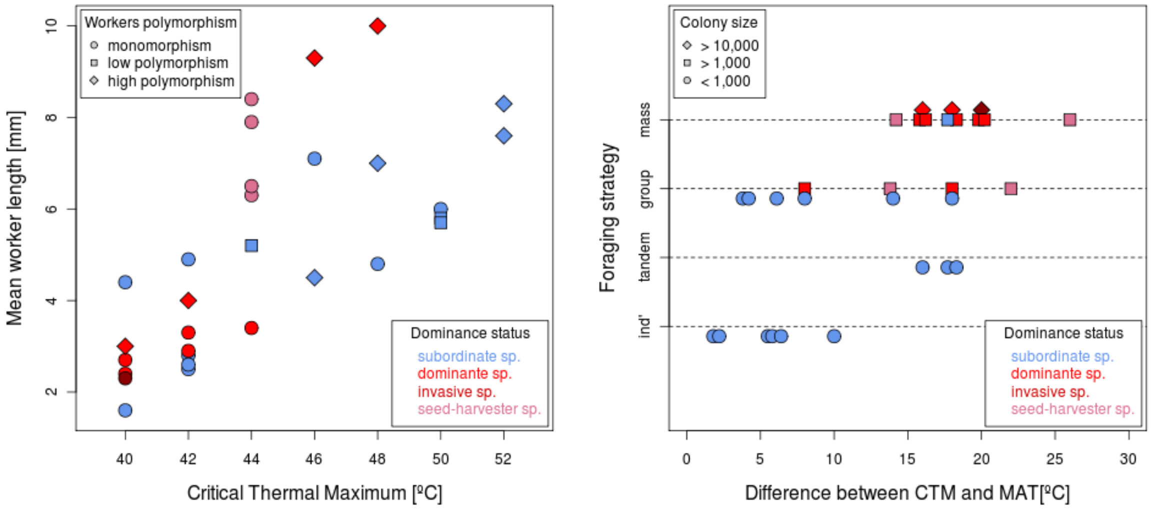
- *Subordinate* species are driven away from baits.

- *Seed-harvester* species belong to the genus *Messor*, and feed only on seeds (Cerdá and Retana, 1994). In natural condition, they do not compete directly with other ant species (that are mainly scavenger, nectarivorous or honeydew-feeding ants).

Table 1.3 — Life-history traits of some Mediterranean ant species (adapted from Cerdá and Retana, *In prep.*). Daily activity rhythms: D, diurnal; DC, diurnal in spring and continuous or with a midday drop in summer; CN, continuous in spring and nocturnal in summer; N, nocturnal. CTM, critical thermal maximum (°C). MAT, maximum activity temperature (°C). Workers polymorphism: a, monomorphism; b, low polymorphism; c, high polymorphism; d, dimorphism. Workers number: a, hundreds; b, thousands; c, tens of thousands. Queens number: monogyny (single queen), polygyny (several queens). Nests number: monodomy (single nest), polydomy (several nests).

SPECIES	DOMINANCE STATUS	FORAGING STRATEGY	WORKERS AT BAIT	DAILY RHYTHM	PEAK OF ACTIVITY	CTM [°C]	MAT [°C]	WORKER LENGTH [mm]	WORKER POLYMORPHISM	WORKER NUMBER	QUEEN NUMBER	NEST NUMBER	MAIN DIET
Dolichoderinae													
Linepithema humile	inv	mass	40	CN	September	40	20	2,4	a	c	polygyny	polydomy	honeydew, nectar
Tapinoma nigerrimum	dom	mass	43	CN	June	42	24	4	c	c	polygyny	polydomy	honeydew, insects
Formicinae													
Camponotus cruentatus	dom	group	8	DC	July	48	40	10	c	b	monogyny	monodomy	honeydew, nectar
Camponotus foreli	sub	group	6	D	August	48	44	7	c	a	monogyny	polydomy	nectar, honeydew
Camponotus piceus	sub	group	4	D	July	44	30	5,2	b	a	monogyny	monodomy	nectar, honeydew
Camponotus sylvaticus	dom	group	9	N	August	46	28	9,3	c	b	monogyny	monodomy	honeydew, nectar
Cataglyphis cursor	sub	ind	3	D	July	50	48	5,8	b	a	monogyny	monodomy	insects, nectar
Cataglyphis floricola	sub	ind	2	D	July	50	44	6	a	a	monogyny	monodomy	insects, nectar
Cataglyphis iberica	sub	ind	3	D	July	52	50	7,6	c	a	monogyny	polydomy	insects, nectar
Cataglyphis rosenhaueri	sub	ind	1	D	July	50	44	5,7	b	a	monogyny	polydomy	insects, nectar
Cataglyphis velox	sub	ind	2	D	July	52	46	8,3	c	a	monogyny	monodomy	insects, nectar
Formica subrufa	sub	group	7	D	July	48	40	4,9	a	a	monogyny	monodomy	insects, nectar
Plagiolepis pygmaea	sub	group	9	CN	May	40	22	1,6	a	a	polygyny	monodomy	nectar, honeydew
Proformica nasuta	sub	ind	3	D	June	46	36	4,5	c	a	monogyny	monodomy	insects, nectar
Myrmicinae													
Aphaenogaster gibbosa	sub	group	15	D	July	42	36	4,9	a	a	monogyny	monodomy	insects, seeds
Aphaenogaster senilis	sub	group	11	D	June	46	42	7,1	a	a	monogyny	monodomy	insects, seeds
Crematogaster auberti	dom	mass	33	CN	July	44	24	3,4	a	b	monogyny	monodomy	nectar, honeydew
Crematogaster sordidula	dom	mass	24	CN	May	40	20	2,5	a	b	monogyny	monodomy	nectar, honeydew
Messor barbarus	seed	mass	12	DC	September	44	18	7,9	c	b	monogyny	monodomy	seeds
Messor bouvieri	seed	group	26	D	September	44	30	6,3	b	b	monogyny	monodomy	seeds
Messor capitatus	seed	group	15	DC	October	44	22	8,4	c	b	monogyny	monodomy	seeds
Messor lusitanicus	seed	mass	25	D	September	44	30	6,5	b	b	monogyny	monodomy	seeds
Myrmica sabuleti	sub	mass	17	N	June	40	22	4,4	a	b	polygyny	monodomy	insects, seeds
Pheidole pallidula	dom	mass	55	CN	September	40	24	3	d	c	monogyny	monodomy	insects, seeds
Temnothorax kraussei	sub	tandem	2	CN	June	42	26	2,8	a	a	monogyny	monodomy	nectar, insects
Temnothorax specularis	sub	tandem	2	CN	June	42	24	2,5	a	a	monogyny	monodomy	nectar, insects
Temnothorax unifasciatus	sub	tandem	2	CN	June	42	24	2,5	a	a	monogyny	monodomy	nectar, insects
Tetramorium caespitum	dom	mass	50	CN	July	42	26	2,9	a	b	monogyny	monodomy	insects, seeds
Tetramorium inpurum	dom	mass	60	CN	July	42	24	3,4	a	b	monogyny	monodomy	insects, seeds
Tetramorium semilaeve	dom	mass	61	CN	June	40	24	2,6	a	b	polygyny	monodomy	insects, seeds

Competitive outcomes are linked to shared ecological characteristics (Fig. 1.4). As widely documented in Mediterranean communities, dominant and subordinate species differ in their physiological tolerance to temperature (Cerdá et al., 1997, 1998b,c,b). Dominant species tend to be less tolerant to high temperatures. They are globally characterised by a lower Critical Thermal Maximum (CTM) (calculated as the lowest temperature at which 50% of the 10 min exposed workers lost muscular coordination). Since larger workers are less subject to dessication (Lighton and Feener, 1989), the positive correlation between temperature tolerance and workers size was expected. Apart from the two highly polymorphic *Camponotus* species, dominants tend to have smaller workers than subordinate (Fig. 1.4a).



(a) (b)

Figure 1.4 — Do life-history traits trade-off in Mediterranean ant communities? a/ Correlation between the mean workers length and the Critical Thermal Maximum according to the level of polymorphism and the dominance status. Estimated Pearson's product-moment correlation coefficient: 0.70 (df=28, p-value < 0.001). b/ Interaction between foraging strategy, colony size dominance status and thermophyly. Species names are detailed in Table 1.3. X-axis represents the difference between the physiological thermal limit (CTM) and the temperature of maximal activity (MAT) of the species. Y-axis represents the foraging strategy of the species with increasing degree of cooperation: individual foraging, tandem running, group recruitment and mass recruitment.

The difference between the CTM and the Maximal Activity Temperature (MAT) is even more discriminant between dominant and subordinate species (Fig. 1.4b). Dominants forage at temperatures far from their critical limit while subordinates forage in a temperature range closed to their CTM (Cerdá et al., 1998a). This difference in thermophyly seems associated with the foraging strategy (Ruano et al., 2000). Thermophyly would be negatively related to the degree of communication used while foraging (Fig. 1.4b). The foraging strategy is also linked to colony size (Beckers et al., 1989). In Mediterranean communities, dominants tend to have more populated colonies and to use collective foraging strategies to exploit rich and stable food sources such as aphids honeydew. Subordinate species have smaller colonies and use more individual strategies to exploit ephemeral resources. The interplay between competitive ability, temperature tolerance, and foraging strategy might thus be a structuring force of Mediterranean ant communities.

1.3 Objectives

1.3.1 Hypothesis

As Hutchinson (1959) about terrestrial diversity, we might wonder why there are so many foraging strategies in Mediterranean ant communities? My general hypothesis is that all these strategies are optimal adaptations to Mediterranean environments. I test this hypothesis from two different perspectives: On the one hand, I focus on the interplay between foraging strategies and Dominance-Discovery trade-off, and I explore how the trade-off might have shaped the evolution of foraging strategies in ant communities. On the other hand, I study how foraging strategies contribute to the Dominance-Thermal tolerance trade-off.

1.3.2 Structure

This dissertation is divided into two autonomous parts:

① The first part deals with the Dominance-Discovery trade-off. This part is fully theoretical. Scenarios of the evolutionary dynamics of foraging strategies are modelled with the adaptive dynamics framework (briefly presented in chapter 2). Theoretical studies (chapters 3 & 4) explore how far the Dominance-Discovery trade-off can explain the emergence and the coexistence of different strategies in a sympatric community. Chapter 5 discusses the significance and limits of the predicted outcomes.

② The second part focuses on the Dominance-Thermal tolerance trade-off. This part is mostly experimental and tests the effect of high temperature on the foraging decisions in three Mediterranean ant species: *Tapinoma nigerrimum* , *Aphaenogaster senilis* and *Lasius grandis*. Chapter 6 & 7 test the hypothesis that high temperatures negatively affect collective foraging through pheromone decay. Chapter 8 tests the dependence of thermophile behaviour on the state of the colony. Chapter 9 assesses the experimental results and some remaining questions.

General conclusions and further prospects are discussed in chapter 10.

Part I

The Discovery-Dominance Trade-off

Introduction

In this part, we focus on the Dominance-Discovery trade-off in ant communities. As defined in the general introduction (see 1.2.2), the Dominance-Discovery trade-off occurs at the community level. It describes the fact that the species who are the first in encountering the food sources are weak competitors: these first discoverers are unable to monopolise or dominate the resource with respect to other species.

Our general hypothesis is to attribute the Discovery-Dominance trade-off to constraint investment of the foragers between the scouts and the recruits.

Scouts (or patrollers) individually search for food while recruits are directed to the food source by nestmates. In some species, scouts explore new regions before recruiting nestmates (Gordon, 1988), and searching individuals adjust their exploratory path to optimize the discovery rate of the colony as a whole (Gordon, 1995). In pharaoh ants (*Monomorium pharaonis*), the scouts (or pathfinder) represent 18 % of the pool of foragers and show higher ability to detect long-lived pheromone trails than other foragers (Jackson et al., 2007). In harvester ants (seed-eating ants like *Pogonomyrmex* sp.), the scouts set the foraging direction by depositing a chemical secretion on one of the existent trails (Gordon, 1988). This activated trail does not lead to a particular food source, but to the foraging area selected by the scouts (Greene and Gordon, 2007a). The scout decision of laying a recruitment trail is ruled by the possibility of ingesting a threshold volume (Mailleux et al., 2000) and might depend on previous experience (Howard et al., 1996) and colony-state (Portha et al., 2004). The recruits remain in the nest, doing nothing (Schmid-Hempel, 1990), ready to be recruited and exploit the resources as soon as the information acquired by the scouts reaches the colony.

The scout dilemma has been theoretically explored. Many authors focus on the optimal balance between discovers and followers (Johnson et al., 1987), scouts and collectors (Jaffe and Deneubourg, 1992), active and inactive (Anderson, 2001), or pro-active and re-active (Dechaume-Moncharmont et al., 2005). All these studies agree on the importance of the environment (food size and density) and the number of workers in the colony.

In this work, we focus on the evolutionary dynamics of this scout dilemma. For this purpose, we use the adaptive dynamics framework we succinctly present in chapter 2. In chapter 3, we analyse the outcome of a model with a fixed number of workers in the colony. This assumption is released in chapter 4 allowing a new definition of colony fitness. Concluding remarks about theoretical models, and predicted outcomes are provided in chapter 5.

CHAPTER 2

Elements of Adaptive Dynamics

2.1 Introduction

Adaptive Dynamics is a quantitative approach for the study of evolutionary processes. This term regroups a large variety of modelling approaches (Abrams et al., 1993; Metz et al., 1996; Dieckmann and Law, 1996; Hofbauer and Sigmund, 1998; Michod, 1999; Vincent and Brown, 2005; Dercole and Rinaldi, 2008). These different perspectives might be grossly categorised into either the "American" or the "European" school. The basic distinction I make between these two approaches depends on the differences between the population dynamics and evolutionary timescales. Practically, the "American" Adaptive Dynamics, also called "Darwinian dynamics" by some authors, considers that both population dynamics and strategy dynamics might fluctuate at a similar timescale (Vincent and Brown, 2005). On the other hand, the "European" Adaptive Dynamics assumes mutations to be rare, deriving thus the strategy dynamics at the evolutionary timescale from the population dynamics at the ecological timescale (Dercole and Rinaldi, 2008). I adopted the "European" perspective of the adaptive dynamics because it adapts better to assumptions in our biological system.

In this chapter, I present some keys to Adaptive Dynamics. I do not pretend to demonstrate formally the whole framework. I just aim to expose a few basic ideas underpinning the mathematical background. I introduce the main logical arguments and illustrate the basic concepts. This chapter is limited to clonal reproduction. The unique source of variability comes from mutations that are assumed to occur on a time scale which is very long relatively to the time scale of interactions between individuals, i.e. the evolutionary timescale is very long relatively to the ecological timescale.

2.2 Invasion Fitness

The underlying idea of Adaptive Dynamics is to consider a resident community and to predict mutant invasion scenarios. The fate of mutants can be inferred from the *Invasion Fitness* function defined as the growth rate of a very rare mutant population in a community composed of residents. What follows justifies the definition and the importance of the Invasion Fitness.

We assumed the resident community to be composed of a single monomorphic population with n individuals characterised by a continuous adaptative trait x. We note $f_R(n, x)$ the per-capita population growth rate. The resident population dynamics is given by the following differential equation:

$$\frac{dn}{dt} = n f_R(n, x) \tag{2.1}$$

Since mutations are assumed to be rare, the resident population reaches its dynamical equilibrium before mutant apparition. For explanation convenience, we assume the resident population dynamics to have a stable equilibrium $n^*(x) > 0$. More complex dynamics such as limit cycles are beyond the scope of this chapter but can also be analysed (Dercole and Rinaldi, 2008). By definition, to be a stable equilibrium in a resident population, $n^*(x)$ must verify the following conditions:

$$\begin{aligned} f_R(n^*(x), x) &= 0 \\ \left.\frac{\partial f_R(n, x)}{\partial n}\right|_{n=n^*(x)} &< 0 \end{aligned} \tag{2.2}$$

The possibility for a mutant to settle in a resident community and eventually to replace the former resident relies on the Resident-Mutant community dynamics. The Resident-Mutant community model is composed of a resident monomorphic population with n individuals characterised by a continuous adaptative trait x, and a mutant population with n' individuals with trait x'. The two populations n and n' interact. We note $f(n, n', x, x')$ the per-capita population growth rate of the resident population. The growth rate of the mutant population $f(n', n, x', x)$ is obtained by exchanging population abundances and trait values. The Resident-Mutant community dynamics is then described by the following system:

$$\begin{cases} \dfrac{dn}{dt} = n f(n, n', x, x') \\ \dfrac{dn'}{dt} = n' f(n', n, x', x) \end{cases} \tag{2.3}$$

The pair $(n = n^*(x), n' = 0)$ is a trivial equilibrium of system 2.3. Its stability is determined by the eigenvalue of the Jacobian matrix estimated at this equilibrium:

$$J_{(n^*(x),0)} = \begin{pmatrix} f(n^*(x), 0, x, x') + n^*(x)\frac{\partial f(n,0,x,x')}{\partial n}\big|_{n=n^*(x)} & [...] \\ 0 & f(0, n^*(x), x', x) \end{pmatrix} \tag{2.4}$$

In the absence of mutants ($n' = 0$), the Resident-Mutant system degenerates necessarily into the Resident-model leading to the equivalence $f(n, 0, x, x') = f_R(n, x)$. Jacobian $J_{(n^*(x),0)}$ might thus be simplified according to conditions 2.2.

$$J_{(n^*(x),0)} = \begin{pmatrix} n^*(x)\frac{\partial f_R(n,x)}{\partial n}\big|_{n=n^*(x)} & [...] \\ 0 & f(0, n^*(x), x', x) \end{pmatrix} \tag{2.5}$$

From conditions 2.2, the first eigenvalue of $J_{(n^*(x),0)}$ $(n^*(x)\frac{\partial f_R(n,x)}{\partial n}|_{n=n^*(x)})$ is negative. The second eigenvalue $\mathcal{S}_x(x')$ is called *invasion eigenvalue* or *invasion fitness*:

$$\mathcal{S}_x(x') = f(0, n^*(x), x', x)$$

Its sign determines the equilibrium stability. If $\mathcal{S}_x(x')$ is negative, the equilibrium $(n = n^*(x), n' = 0)$ is a stable attractor of the Resident-Mutant system. In this case, the mutant population goes extinct. Conversely, if $\mathcal{S}_x(x')$ is positive, mutant extinction is not a stable attractor of the Resident-Mutant system: the mutant population invades. If $\mathcal{S}_{x'}(x)$ is negative, then the pair $(0, n^*(x'))$ is a stable equilibrium and the mutant population becomes the new resident population. On the other hand, if $\mathcal{S}_{x'}(x)$ is also positive, the two populations coexist in the community.

2.3 Canonical equation

Several investigations on coevolutionary processes have demonstrated that the dynamics of trait x at the evolutionary timescale could be written as an ODE called *canonical equation* (Eq. 2.6). This equation involves the mutational rate ($k(x)$) and the invasion gradient:

$$\dot{x} = k(x)\frac{\partial \mathcal{S}_x(x')}{\partial x'}\bigg|_{x=x'} \tag{2.6}$$

The following part briefly introduces some ideas underlying the statement of this canonical equation. The arguments we present were first proposed by Dieckmann and Law (1996). A more formal mathematical approach demonstrated that this canonical equation could be extended to a more general case with biased mutation step distribution (Champagnat et al., 2001).

Evolutionary change is a stochastic process. The determinist description of $\dot{x}$ is interpreted as the average among all possible realisations:

$$\dot{x} = \lim_{dt \to 0} \frac{\mathbb{E}[x(t+dt) - x(t)]}{dt} \tag{2.7}$$

where t spans the evolutionary timescale. By definition of the expected value (operator $\mathbb{E}[.]$), equation (2.7) can be expressed with the probability function $\mathbb{P}(x, x', dt)$ for a population with trait x at t to be characterised by trait x' at time $t + dt$.

$$\dot{x} = \lim_{dt \to 0} \frac{1}{dt} \int_{-\infty}^{+\infty} (x' - x)\mathbb{P}(x, x', dt) dx' \tag{2.8}$$

$\mathbb{P}(x, x', dt)$ designates the co-occurrence of three events: i/ a mutation occurs between t and $t + dt$; ii/ the mutant trait value is between x' and $x' + dx'$ iii/ the mutant trait substitutes the resident. Condition (i) depends on the number of individuals in the population $n^*(x)$, the per capita birth rate, and the fraction of birth giving rise to mutation $\mu(x)$. From mutation process symmetry, condition (ii) relies on the variance of the mutation probability distribution $\sigma^2(x)$. Condition (iii) depends on the invasion fitness of the mutant: if the invasion fitness is negative, the probability to escape initial extinction is null; if the invasion fitness is positive, this probability might be analytically calculated from both the per capita birth rate and the invasion fitness. Further developments of equation (2.8) lead to the complete expression (Dieckmann, 1997; Dercole and Rinaldi, 2008):

$$\dot{x} = \frac{1}{2}\mu(x)\sigma^2(x)n^*(x) \left. \frac{\partial \mathcal{S}_x(x')}{\partial x'} \right|_{x=x'} \tag{2.9}$$

This canonical equation is useful to demonstrate the robustness of the Adaptive Dynamics framework when considering stochastic mutations. However, the evolutionary dynamics might be approached from different perspectives such as the geometrical study of Metz et al. (1996). Since we aim to present Adaptive Dynamics as intuitively as possible, we do not use the canonical equation in our later development. Note that the conclusions would have been strictly identical if we had started from the canonical equation (see Dercole and Rinaldi (2008) for full demonstration).

2.4 Evolutionary dynamics in a monomorphic community

The evolution of trait x results from a sequence of mutation-invasion steps. This discrete process might be converted into a continuous process by considering small and rare mutations. Since the monomorphic community is considered at equilibrium, the invasion fitness of an individual with the same trait value is null ($\mathcal{S}_x(x) = 0$). For trait values x' very close to x, the invasion fitness might thus be approximated linearly:

$$\lim_{x' \to x} \mathcal{S}_x(x') = \left.\frac{\partial \mathcal{S}_x(x')}{\partial x'}\right|_{x'=x} (x' - x) \tag{2.10}$$

Regarding small mutations, the direction of evolutionary changes is thus given by the so called *invasion gradient* $\frac{\partial \mathcal{S}_x(x')}{\partial x'}|_{x'=x}$. If the invasion gradient is positive (resp. negative), a small increase (resp. a decrease) of the trait value x is at advantage.

Trait values for which the invasion gradient vanishes ($\frac{\partial \mathcal{S}_x(x')}{\partial x'}|_{x'=x} = 0$) are called *singular strategies* (SS). These values are the equilibria of the trait dynamics (see equation 2.6). Let x^* be a SS. To understand what happens at this given point, we proceed to a quadratic approximation:

$$\lim_{x' \to x^*} \mathcal{S}_{x^*}(x') = \left.\frac{\partial^2 \mathcal{S}_{x^*}(x')}{\partial x'^2}\right|_{x'=x^*} (x' - x^*)^2 \tag{2.11}$$

When $\frac{\partial^2 \mathcal{S}_{x^*}(x')}{\partial x'^2}|_{x'=x^*} < 0$, the invasion fitness is negative, and the mutant population extinguishes. In this case, the SS is called an *Evolutionary Stable Strategy* (ESS): no nearby mutants can invade the resident population (Maynard Smith, 1974).

The second main question the Adaptive Dynamics allows to answer deals with the evolutionary convergence of the SS: if a resident population has a strategy x closed to x^*, will successful mutant strategies be nearer to x^*? For a monomorphic community to approach the SS x^*, the invasion gradient should be positive for $x < x^*$ and negative for $x > x^*$. Thus, the derivative of the selection gradient should be negative:

$$\frac{\partial}{\partial x}\left(\left.\frac{\partial \mathcal{S}_x(x')}{\partial x'}\right|_{x'=x}\right)\Bigg|_{x=x^*} = \left(\frac{\partial^2 \mathcal{S}_x(x')}{\partial x'\,\partial x} + \frac{\partial^2 \mathcal{S}_x(x')}{\partial x'^2}\right)\Bigg|_{x=x'=x^*} \tag{2.12}$$

When this quantity is negative (resp positive), the SS is convergence stable (resp. unstable). This means that the SS acts as an evolutionary attractor (resp. repellor): strategies closed to this SS will evolve toward this point (Christiansen, 1991).

Table 2.1 summarises these two conditions. More properties might though be defined to establish an exhaustive list (Geritz et al., 1998; Diekmann, 2004).

Table 2.1 — Main strategy properties

PROPERTIES		MATHEMATICAL CONDITIONS
SS	Singular Strategy	$\frac{\partial \mathcal{S}_{x^*}(x')}{\partial x'}\|_{x'=x^*} = 0$
ESS	Evolutionary Stable Strategy	$\frac{\partial^2 \mathcal{S}_{x^*}(x')}{\partial x'^2}\|_{x'=x^*} < 0$
CSS	Convergence Stable Strategy	$\frac{\partial^2 \mathcal{S}_x(x')}{\partial x'\,\partial x}\|_{x=x'} + \frac{\partial^2 \mathcal{S}_x(x')}{\partial x'^2}\|_{x=x'} < 0$

The evolution of a monomorphic community can be inferred from the shape of the *Pairwise Invasibility plot* (Fig. 2.2). This graphical tool represents the sign of the invasion fitness $S_x(x')$ as a function of x and x'. In the regions where the invasion fitness is positive (shaded areas in Fig. 2.2), mutants can spread. The first diagonal represent the line $x = x'$. The Singular Strategies correspond to the intersection between the first diagonal and the contour $S_x(x') = 0$. Their properties can be predicted according to the shape of the positive (resp. negative) areas at its neighbourhood.

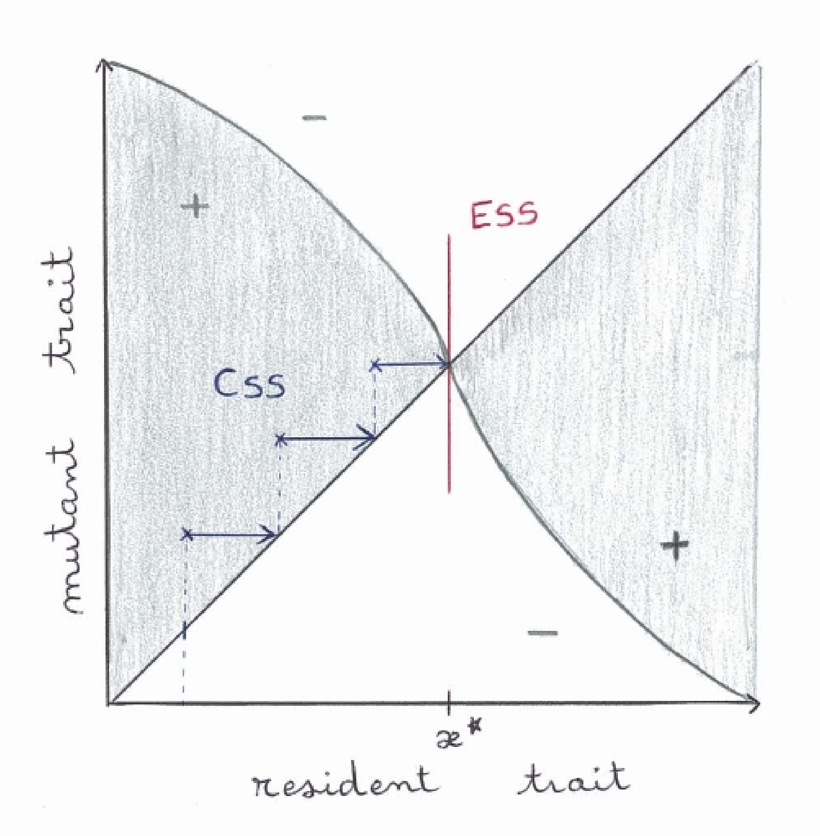


Figure 2.2 — Pairwise Invasibility Plot illustrates both ESS & CSS properties. The shaded areas represent a combination of both resident and mutant trait values for which mutant's invasion fitness is positive. A monomorphic state of a resident community is a point of the main diagonal. Successful mutants invade and become the new resident population until reaching the singular strategy x^* (CSS). Once the resident strategy is x^*, all mutant strategies have a negative invasion fitness, i.e. no mutant can invade (ESS)

The combination of properties defines the four main categories of Singular Strategies (Table 2.3). An *ending point* acts as a final stop of evolution (e.g. Fig. 2.2): attractor of bidirectional evolution (CSS), it cannot be invaded by nearby mutants (ESS). Ending points are continuously stable strategies sensu Eshel (1983). Conversely, *evolutionary repellors* are traits that experience a minimum of the fitness landscape (~~ESS~~) and gradual adaptations evolve away from those strategies (~~CSS~~). Evolutionary repellors separate the basins of attraction of adjacent SS. A SS is called *garden of eden* when the value is a local maximum of the fitness landscape, i.e. no nearby mutant can invade (ESS), but directional evolution leads away from this trait (~~CSS~~). *Branching points* present a particular interest (Fig 2.4). Processes of gradual adaptation converge toward these traits (CSS), but those strategies are local minima of the fitness landscape (~~ESS~~). Mutant phenotypes have a fitness advantage over the intermediate resident phenotype. Disruptive selection gives rise to a protected dimorphism: two populations with distinct phenotypes coexist in the community.

Table 2.3 — Classification of the Singular Strategies

EVOLUTIONARY OUTCOMES	PROPERTIES		
Ending point	ESS	&	CSS
Evolutionary Repellor	~~ESS~~	&	~~CSS~~
Garden of Eden	ESS	&	~~CSS~~
Branching point	~~ESS~~	&	CSS

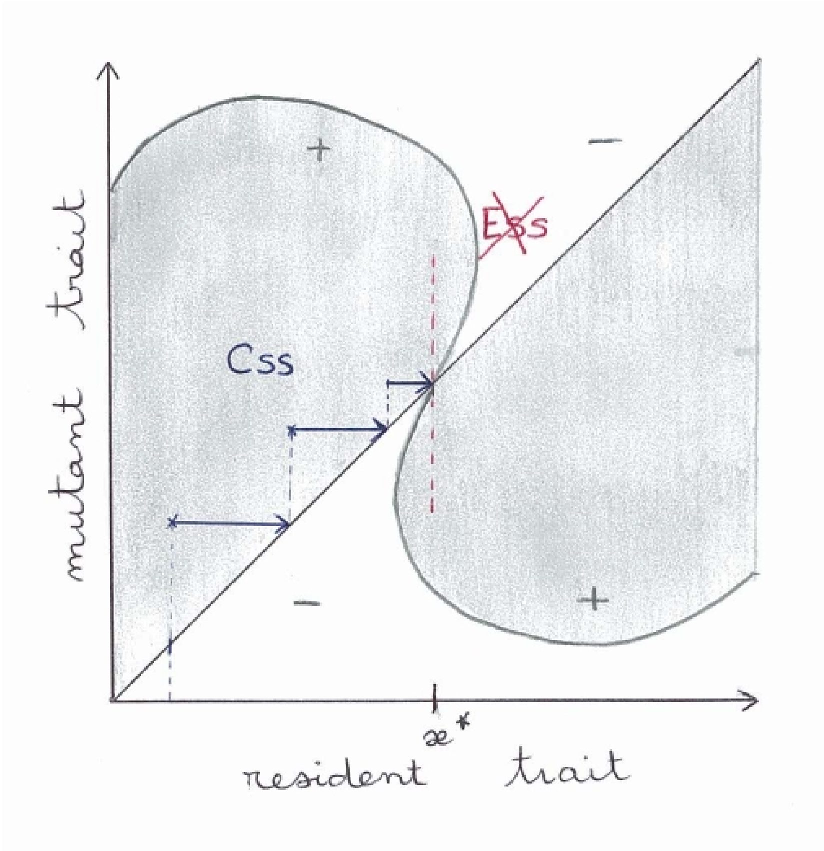


Figure 2.4 — Pairwise Invasibility Plot of a branching event. Successful mutants invade, leading progressively the resident trait toward the singular strategy x^* (CSS). Once the resident strategy is x^*, nearby mutants have a positive invasion fitness, i.e. they can invade (~~ESS~~)

Evolutionary branching are scenarios that explain how higher levels of polymorphism enter a sympatric community via negative frequency-dependent selection. Notwithstanding, as judiciously asked by Rueffler et al. (2006), "disruptive selection, and then what?" The evolutionary outcomes depend at present on the dimorphic community dynamics.

2.5 Evolutionary dynamics in a dimorphic community

As in the monomorphic case, gradual adaptation processes drive the phenotypic diversity of the community. However, in this case, the resident community is composed of two trait values x_1 and x_2. The number of individuals of each phenotype $n_1(x_1, x_2)$ and $n_2(x_1, x_2)$ are assumed to be equilibria of the system 2.3:

$$\begin{cases} f(n_1(x_1,x_2), n_2(x_1,x_2), x_1, x_2) = 0 \\ f(n_2(x_1,x_2), n_1(x_1,x_2), x_2, x_1) = 0 \end{cases} \tag{2.13}$$

The invasion fitness in a dimorphic resident community is defined as the fitness of a scarce mutant in a resident community at equilibrium. In a similar way as in the case of a monomorphic resident community, it derives from a Resident-Mutant matrix. We note $F(n_a, n_b, n_c, x_a, x_b, x_c)$ the growth rate of the a-population in a community composed of n_a, n_b, and n_c individuals with respective phenotypes x_a, x_b, and x_c. Consequently, $F(n_a, n_b, 0, x_a, x_b, x_c) = f(n_a, n_b, x_a, x_b)$ and the invasion fitness of a mutant with trait x' in the dimorphic community becomes:

$$S_{x_1,x_2}(x') = F(0, n_1(x_1,x_2), n_2(x_1,x_2), x', x_1, x_2) \tag{2.14}$$

Similarly as in the monomorphic case, if this invasion fitness is negative ($S_{x_1,x_2}(x') < 0$), mutant goes extinct. Conversely, if $S_{x_1,x_2}(x') > 0$, four scenarios are conceivable: i/ (resp. ii/) mutant trait replaces the resident trait x_1 (resp. x_2), and the community remains dimorphic; iii/ mutant trait replaces the two resident traits, and the community becomes monomorphic again; iv/ mutant trait coexists with the two resident traits, and the community reaches a higher degree of polymorphism.

Since mutations are rare, they are assumed to occur only once at a time, either on trait x_1 or on trait x_2. For trait values x' very close to x_i ($i \in \{1,2\}$), the invasion fitness might thus be approximated linearly:

$$\lim_{x' \to x_i} \mathcal{S}_{x_1,x_2}(x') = \left. \frac{\partial S_{x_1,x_2}(x')}{\partial x'} \right|_{x'=x_i} (x' - x_i) \tag{2.15}$$

Two fitness gradients are defined: $\frac{\partial S_{x_1,x_2}(x')}{\partial x'}\Big|_{x'=x_1}$ and $\frac{\partial S_{x_1,x_2}(x')}{\partial x'}\Big|_{x'=x_2}$. Particular point x^* where these fitness gradients vanish are called *Evolutionary Isoclines* (see Fig. 2.5), either x_1 or x_2-isoclines.

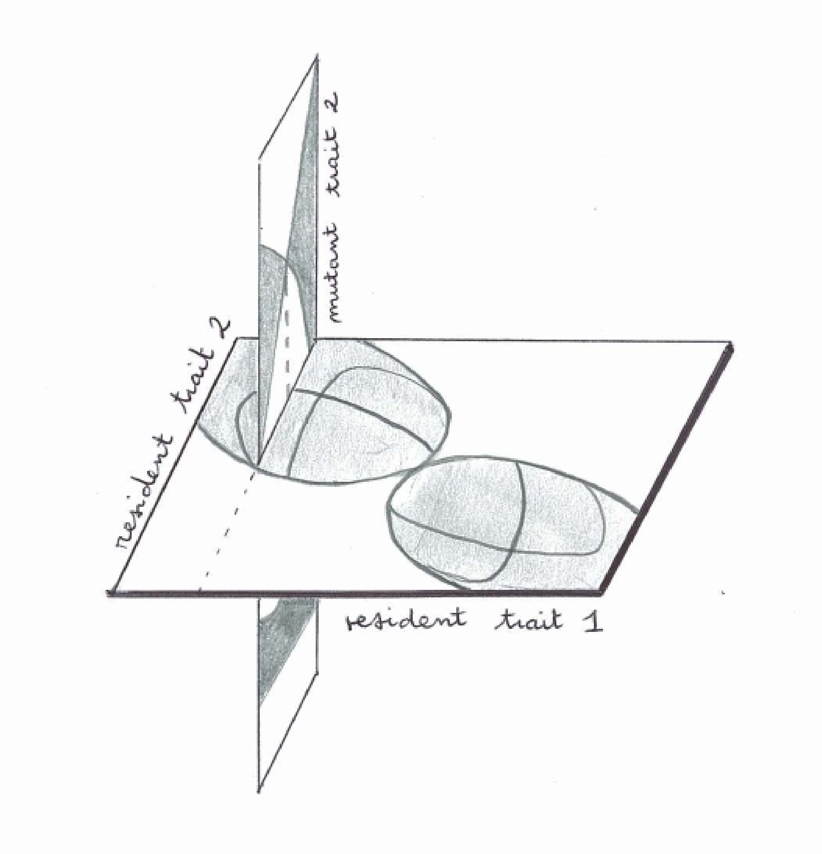


Figure 2.5 — Evolutionary isoclines represent the Singular Strategies in a dimorphic community. The shaded region are the area of coexistence of the two resident traits. They are plotted by overlapping a Pairwise Invasibility Plot and it's mirror image over the diagonal. The third dimension represents a Pairwise Invasibility Plot of mutant-resident trait 2 for a given resident trait 1. Evolutionary isoclines are projections of the singular strategies of all the possible mutant-resident Pairwise Invasibility Plot.

In the neighbourhood of an x_i-isocline, the sign of the mutant invasion fitness is determined by a quadratic approximation:

$$\lim_{x' \to x_i} \mathcal{S}_{x_1,x_2}(x') = \left. \frac{\partial^2 S_{x_1,x_2}(x')}{\partial x'^2} \right|_{x'=x_i} (x' - x_i)^2 \tag{2.16}$$

If $\frac{\partial^2 S_{x_1,x_2}(x')}{\partial x'^2}\Big|_{x'=x_i} < 0$ (resp. > 0), the x_i-isocline corresponds to a local fitness maximum (resp. minimum). Practically, analytical determination and classification of evolutionary isoclines is often difficult. However, their graphical representation can be inferred from the shape of the area of coexistence. This region represents the set of values likely to coexist in a protected dimorphism. Graphically, this area is obtained by overlapping the Pairwise Invasibility Plot of x_1 according to x_2 with these of x_2 according to x_1 (Fig. 2.5 & 2.6).

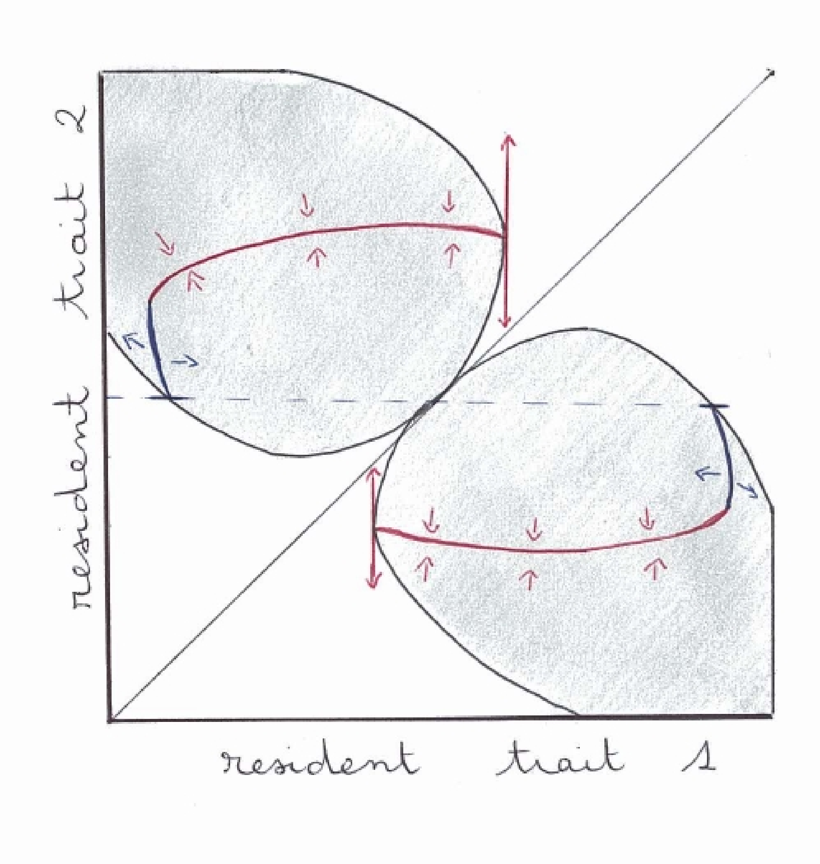


Figure 2.6 — Graphical determination of the x_2-Isocline. The method used is described in the Table 2.7. Shaded regions represent the area of coexistence of the two resident strategies. Isoclines that represent a fitness maximum (resp. minimum) are plotted in red (resp. blue).

Table 2.7 — How to build Evolutionary Isoclines? This table sum up the graphical keys presented by Geritz et al. (1999)

CONNECTION POINTS	LOCAL FITNESS MAXIMUM OR MINIMUM?			
x_2-Isoclines				
where the boundary has a vertical tangent	boundary locally	convex	→	max
		concave	→	min
horizontally above a Singular Strategy	inherit SS properties	ESS	→	max
		~~ESS~~	→	min
x_1-Isoclines[1]				
where the boundary has an horizontal tangent	boundary locally	convex	→	max
		concave	→	min
vertically above a Singular Strategy	inherit SS properties	ESS	→	max
		~~ESS~~	→	min

[1] might also be deduced from the x_2-Isoclines by mirror image over the diagonal

There are no analytical classifications of the evolutionary scenarios once the population has become dimorphic. Evolutionary dynamics might though be predicted from the configuration of the Evolutionary Isoclines (Geritz et al., 1999). In particular, at the intersection of an x_1-isocline and an x_2-isocline, directional evolution ceases for both residents. These combinations are called *Evolutionary Singular Coalitions*. Singular coalitions are stable if both isoclines are fitness maxima (Fig. 2.8). In this case, community remains dimorphic, no new mutants will invade. Convergence in dimorphic communities might depend on the respective mutation rates of both residents (Abrams et al., 1993). Nevertheless, like in the monomorphic case, singular coalitions that are convergence stable but lack evolutionary stability (i.e. represent a fitness minima) at least for one of the resident traits, give rise to disruptive selection. In this case, the population undergoes a new branching event, and the community becomes trimorphic.

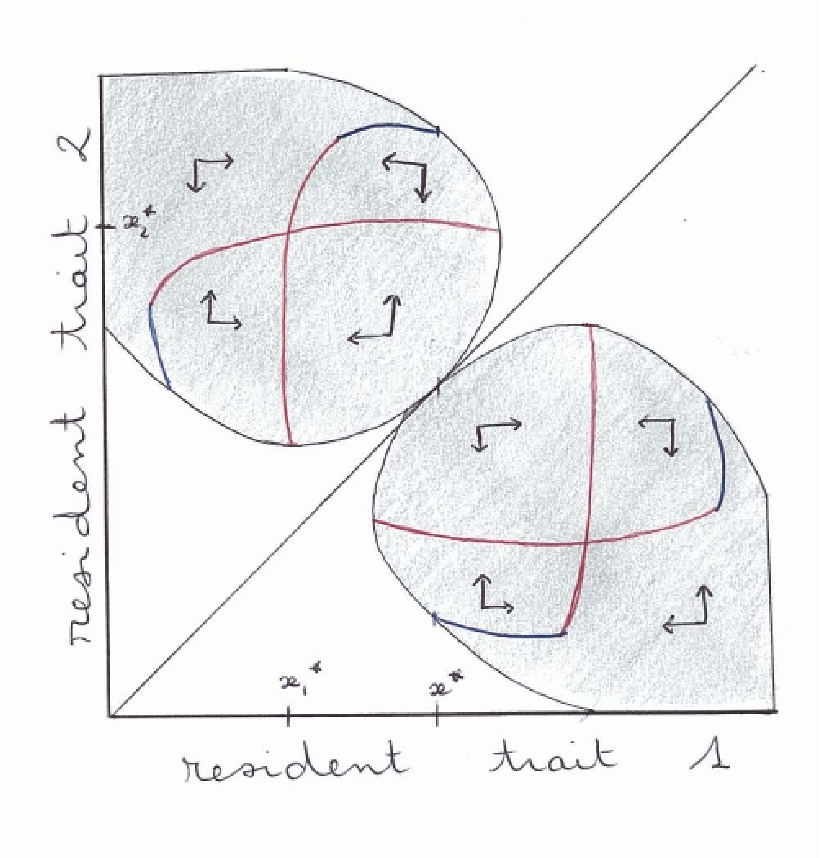


Figure 2.8 — Evolutionary Singular Coalitions are points of intersection between an x_1-isocline and an x_2-isocline. The x_2-isocline was determined in Fig. 2.6, and the x_1-isocline was deduced by symmetry. Singular coalitions occur in symmetric pairs due to the equivalent roles of x_1 and x_2. Since this pair of singular coalition corresponds to the intersection of two fitness maxima, this particular combination of x_1 and x_2 represents a final stop of the evolutionary process.

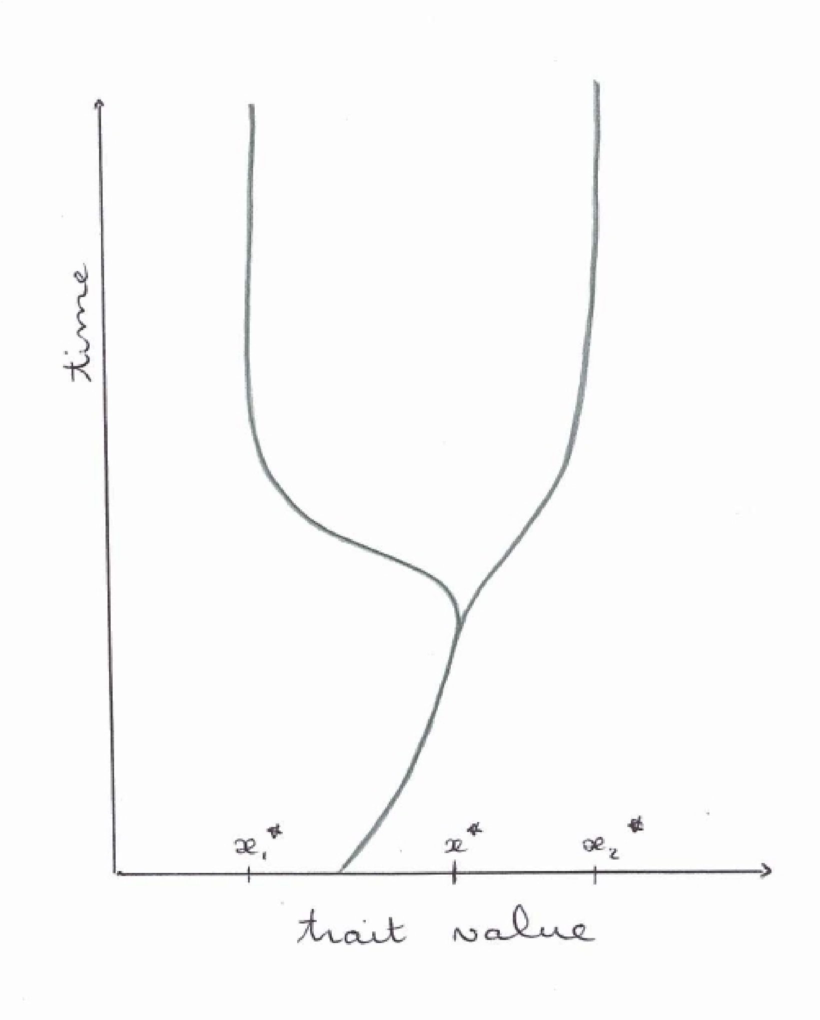


Figure 2.9 — The evolutionary tree represents the scenario predictable by Fig. 2.8. In a monomorphic community, trait value x^* is an attractor of directional evolution. When the branching point x^* is reached, selection turns disruptive. The population becomes dimorphic in the neighbourhood of x^*. The two trait values diverge away until reaching the stable coalition x_1^* and x_2^*.

The association between the phenomenon of evolutionary branching and sympatric speciation events has been widely discussed especially regarding the part played by sexual selection (Dieckmann and Doebeli, 1999; Jansen and Mulder, 1999; Tregenza and Butlin, 1999; Doebeli and Dieckmann, 2000, 2003; Abrams, 2001a; Geritz et al., 2004; van Doorn et al., 2004; van Dooren et al., 2004; Doebeli et al., 2005). These debates are far beyond the scope of this introduction to the Adaptive Dynamics framework. Nevertheless, the idea to retain is that branching events mean the emergence of polymorphism in a sympatric community. They do not necessarily imply the subsistence of polymorphism, but they create coexisting lineages that will co-evolve further.

2.6 Conclusions

Darwin (1859) liked to remember the *old canon in natural history of "Natura non facit saltum"*. This concept of continuity constitutes the main difference between Evolutionary Game Theory and Adaptive Dynamics. Both are mathematical frameworks modelling frequency-dependent selection. The former assumes a finite set of feasible strategies. The latter generalises the concept enabling to understand the evolutionary outcomes of small mutations in traits expressing the phenotype.

This chapter described the tools provided by the Adaptive Dynamics framework and explained how standard models of population dynamics allow the study of long-term phenotypical evolution. Chapters 3 & 4 use Adaptive Dynamics as a toolbox.

CHAPTER 3

Evolutionary dynamics explains social foraging strategy diversity in ant communities [1]

In ant communities, species using different foraging strategies coexist. We develop an adaptive dynamics model to get a better understanding of the factors that promote the apparition and the maintenance of such diversity. We analyse the consequences of both interspecific competition and resource distribution for the evolutionary dynamics of social foraging in ants. The evolution of social foraging behaviour is modelled by a stochastic mutation-selection process relying on the interactions between colonies. Within the community, ant colonies share a same environment characterized by a limited resource. Their interactions depend on the specific foraging strategies (defined as the degree of collective foraging), the distribution of the resource, and the degree of asymmetry in competition. At the ecological timescale, we propose a model of foraging processes that reflects the trade-offs between resource discovery, and both resource exploitation and behavioural dominance. At the evolutionary timescale, we identify the conditions of competition and resource distribution that lead to the emergence and coexistence of both collective and individual foraging strategies. We suggest that asymmetric competition is an essential component of the emergence of diversity of foraging strategies in a sympatric ant community.

---

[1] Co-authors: **X. Cerdá, C. Bernstein**

3.1 Introduction

A foraging strategy is a complex set of behavioural and morphological traits suited to gather food resources in a particular environment (Schoener, 1971). In social foragers, the selective value of a strategy strongly relies on the interdependence of individuals (Giraldeau and Caraco, 2000). In eusocial insects in particular, foragers are sterile and thus released from conflicting investments in reproduction versus other time and energy intensive tasks (Traniello, 1989). This particularity makes eusocial insects an interesting model for the study of social foraging. In ants, foragers do not collect food only for their own consumption, but for that of the whole colony. Consequently, elaborate communication devices might facilitate cooperative foraging (Oster and Wilson, 1978; Hölldobler and Wilson, 1990). Ants show a wide spectrum of foraging strategies: the foragers of a colony range from being completely independent to retrieving food sources only through recruitment (Oster and Wilson, 1978; Deneubourg et al., 1986). Foraging strategies in ants are a continuum of the integration of a single forager into a collective network and might be categorized according to the degree of communication they require (Traniello, 1989; Beckers et al., 1989). Individual or noncooperative foraging does not require communication: each ant searches for food and transports it individually to the colony (Goss et al., 1989). On the other hand, recruitment involves the ant that has discovered a resource alerting inactive nestmates. One of the most communication-intensive strategies is mass recruitment by means of a pheromone trail (Bonabeau et al., 1998a).

Not all ant species can display recruitment behaviour. This ability depends on the morphology and chemical communication capacity of the species (Hölldobler and Wilson, 1990). In ant literature, individual foraging species are commonly referred to as “primitive”, compared to mass recruiting species (Hölldobler and Wilson, 1990). Nonetheless, the evolution of recruitment behaviour in ants remains unclear and cladistic analysis suggests that an increase in recruitment efficiency has been repeatedly selected within different ant clades (Baroni Urbani, 1989, 1993). The hypothesis that differently efficient foraging behaviour have been selected by environmental constraints seems more credible biologically (Baroni Urbani, 1993; Ruano et al., 2000). Ant foraging strategies rely on a series of components that have evolved in response to both intrinsic parameters as colony size (the degree of communication used in foraging seems positively correlated with the size of the colony in many ant species, Beckers et al. (1989)) and external factors such as resource distribution patterns, competition, predation (Traniello, 1989), and abiotic conditions (particularly temperature) (Ruano et al., 2000).

In eusocial insects, optimal foraging behaviour should maximize food return to the colony (Oster and Wilson, 1978). Foraging activity occurs in two steps: the discovery of the resource and its exploitation. The scouts search for food, gather information about resources (Gordon, 1983) and recruit foragers by either direct (e.g. waggle dance in bees, von Frisch (1967)) or indirect (e.g. pheromone laying in ants, Hölldobler and Wilson (1990)) recruitment behaviours. The recruits or collectors remain in the nest, ready to be recruited to exploit the resources as soon as the information conveyed by the scouts reaches the colony. This pool of recruitable workers determines the efficiency of the recruitment process (Deneubourg et al., 1986). At the colony level, the challenge in social foraging is to find the optimal balance between investing in the discovery versus exploitation. Different theoretical studies on the scout-recruit system in social insects predict an optimum proportion of scouts maximizing either the gross (Jaffe and Deneubourg, 1992), or the net gain of the colony (Johnson et al., 1987; Anderson, 2001; Dechaume-Moncharmont et al., 2005). All of them predict that the optimum strategy is strongly linked to the characteristics of the resources. When food items are either small or easy to find, individual foraging is the most efficient strategy (i.e. all foragers are scouts), whereas division of labour is promoted with other kinds of resources. These studies develop models that clarify social insect foraging at the colony level. Nevertheless, none of them take frequency-dependent competition among species into account, even though empirical studies emphasize the importance of both resource characteristics and competitive pressure in understanding ant foraging strategies (Tanner, 2008). The evolution of foraging strategies might thus strongly depend on the strategies adopted by the other colonies of the community.

In some ecosystems, species using different foraging strategies coexist. For instance, in Mediterranean ant communities, individual foraging (e.g. *Cataglyphis cursor*), group foraging (the recruiter returns to the food source guiding a small group of nestmates, e.g. *Aphaenogaster senilis*), and mass recruiting (e.g. *Tapinoma nigerrimum*) species share the same biotope (Cerdá et al., 1997). The explanation for the persistence of such diverse foraging strategies in ant communities remains elusive.

Niche partitioning is likely to play a significant role in promoting ant species coexistence. Co-occurring species often differ in different components of diet such as food type (Sanders and Gordon, 2003; Blüthgen and Fiedler, 2004) and food size (Cerdá et al., 1998b; Lebrun, 2005), daily activity, which is essentially regulated by species thermal tolerance (Vepsäläinen and Savolainen, 1990; Cerdá et al., 1998a; Retana and Cerdá, 2000; Bestelmeyer, 2000; Albrecht and Gotelli, 2001), nesting sites (Torres, 1984), and microhabitat use (Savolainen and Vepsäläinen, 1989; Sanders et al., 2007). Yet, Andersen (2008) suggests that there are "not enough niches" to explain the high species richness of many ant communities . He argues that the majority of generalist ant species have overlapping requirements. Field studies confirm such patterns of niche inclusion (Torres, 1984).

Competitive trade-offs are often thought to promote diversity in communities (Tilman, 1994; Chave et al., 2002; Calcagno et al., 2006). Competitive mechanisms might be distinguished according to the nature of the interactions they involve. Exploitation competition results from the limitation of resources, whereas interference competition is the outcome of direct interactions between organisms (Park, 1962). Ants are subject to a severe trade-off between exploitation and interference capacities: resource discovery and behavioural dominance abilities are negatively correlated (Fellers, 1987; Holway, 1999), and seem to be species-specific characteristics (Jordan and Blüthgen, 2007). Species that successfully defend food against competitors are called dominant, whereas species that are behaviourally subordinate in encounter competition, but show capacities for rapid resource discovery are said to be submissive (Fellers, 1987; Savolainen and Vepsäläinen, 1988; Davidson, 1998). This trade-off might promote ant species coexistence (Perfecto, 1994; Lebrun and Feener, 2007; Adler et al., 2007). Furthermore, the dominance hierarchy is affected by environmental factors such as temperature (Cerdá et al., 1997; Bestelmeyer, 2000) and resource availability (Sanders and Gordon, 2003; Lester et al., 2010). The influence of these environmental variables reduces competitive exclusion (Palmer et al., 2000; Andersen, 2008). Both empirical and theoretical evidence show that the interplay between species-specific characteristics in foraging behaviour and context-dependent asymmetric competition is fundamental in ant community structure (Blüthgen and Fiedler, 2004; Adler et al., 2007). Adler and colleagues explain how the dominance-discovery trade-off maintains the coexistence of species differing in their foraging behaviour. In a very elegant model of food patch occupancy dynamics, they characterise species by resource discovery rate and worker body mass, and then model fully asymmetric interspecific competition by assuming that slower discoverers are dominant over faster discoverers. They show how a set of species with very different discovery rates can coexist in such community (Adler et al., 2007). Many questions on both proximate and ultimate causes are prompted by this work. From a mechanistic stand point: i/ What are the mechanisms underling the trade-off between dominance and discovery abilities? ii/ Is the competition so strongly asymmetric? iii/ What would be the consequence of relaxing the intensity of the competitive trade-off? From a functional point of view: i/ How did evolution allow the establishment of strategy diversity? ii/ Might the dominance-discovery trade-off have favored the emergence of very different foraging strategies?

In this work, we aim to answer these questions by integrating the recruitment strategy into a community level model. As in previous models of social insect foraging at the colony level, the energy intake of colonies will be constrained by a trade-off between the discovery and the exploitation of resources. Nevertheless, as interspecific competition is a key factor of ant community structure (Hölldobler and Wilson, 1990; Parr and Gibb, 2010), we take frequency-dependent competition into account. Moreover, we suggest an explanation to the discovery-dominance trade-off through the use of foraging strategies: as behavioural dominance is positively correlated with numerical dominance (forager density) (Savolainen and Vepsäläinen, 1988; Davidson, 1998), we suggest that success in interference competition depends on the number of foragers exploiting a resource. We examine how the interplay between resource characteristics and the nature of the interactions between species might determine both foraging strategy coexistence at the ecological timescale, and foraging strategy dynamics at the evolutionary timescale. We use an adaptive dynamics framework to test to which extent the double trade-off between discovery and both exploitation and dominance explains the emergence and maintenance of foraging strategy diversity in ant communities.

3.2 The model

Among all the workers of a colony, the pool of foragers are the ants that gather food. Among these foragers, some search for resources by themselves (individual foragers or scouts) while others wait in the nest to be recruited (recruits). A colony might invest more or less in individual foragers or recruits. This investment defines the colony's foraging strategy. The more a colony invests in individual foragers (or scouts), the more efficient it is at resource discovery. The more a colony invests in collective foragers (or recruits), the more efficiently it harvests resources and eventually interferes competitively (Adler et al., 2007). This investment (or foraging strategy) is thus submitted to a trade-off due to the finite number of foragers. The aim of our work is to identify the foraging strategies that would be evolutionarily stable and to determine the conditions under which multiple strategies would coexist as an evolutionary stable combination (a coalition Geritz et al. (2004)).

In this section, we present a simple model of the evolution of foraging strategies in ants sharing the same environment. We start by using differential equations to model the interations between ant colonies for access to nutritive resources. From these interactions, we establish the net rate of energy intake and the fitness of a single colony. From the model of colony dynamics, and using the adaptive dynamics framework (Dieckmann and Law, 1996; Metz et al., 1996), we deduce the long-term evolution of foraging strategies. Lastly, we make explicit the mechanisms involved in the foraging process in order to specify the former dynamics.

All analyses were performed using Wolfram Mathematica 7.

Table 3.1 — Parameters used in the model

SYMBOL	DESCRIPTION
i	Proportion of recruits
q_i	Number of colonies using a strategy i
σ_R	Renewal rate of food items
e_R	Amount of energy available per food item
D_i	Discovering rate
E_i	Exploitation rate
$C_{i,j}$	Probability that a i-colony usurp a patch previously controlled by a j-colony
σ_q	Efficiency of conversion of energy into new colonies
γ	Mortality rate of colonies
ρ	Food items density
w	Number of foragers
l	Ants loading capacity
v	Ants speed
ϕ	Competition strength

3.2.1 The evolutionary model

As we are focusing on the evolution of foraging strategies and wish to simplify a complex situation, we consider each colony as an individual and we assume that all individuals are strictly equivalent in characteristics. In particular, all species share the same colony size whatever their foraging strategy. Each individual is characterized by its strategy x_i, a continuous trait that represents the proportion of foragers that are recruits within foragers. Henceforth, we call species the set of colonies sharing the same strategy i and we denote q_i the number of colonies using this strategy.

Our model is based on three main assumptions: (i) Resources are patchily distributed in the environment. The food items (or patches) are randomly distributed with density ρ; (ii) The total amount of food available in the environment is fixed: the more numerous the food items (i.e. the higher their density), the smaller they are and the pace at which new items appear (i.e. their renewal rate) σ_R is inversely proportional to the amount of energy available per item e_R. Moreover, we assume without loss of generality that the total amount of food in the environment is unity, i.e. the product between food item number and item size is unity, the same as the product between food item renewal rate and the amount of energy per item. (iii) There is no competition with other agents than ants: a food item disappears only if it is consumed by an ant colony.

The first step in understanding an ant community is to focus on the fate of resources (Adler et al., 2007). Let n be the number of species sharing this environment. We distinguish

$(n+1)$ types of food items: R is the number of undiscovered ones, and $R_i,\ i \in [1,n]$ is the number of items discovered and exploited (i.e. "controlled") by a given colony of species i. A colony loses control of an item by exhausting it or by being driven away by a colony of a different species. We assume that changes of "ownership" between colonies of the same species is immaterial for the success of their strategy. In what follows, we make explicit the dynamics of these $(n+1)$ kinds of food items.

Patch dynamics are described in system (3.1). Equation (3.1.a) deals with the dynamics of undiscovered food items. These items appear at rate σ_R, and disappear if discovered by an ant colony. The disappearance rate of R is then the sum of the discovering rates D_i of the q_i colonies of each species. Equation (3.1.b) describes the dynamics of the food items controlled by a colony of species i. The first term of equation (3.1.b) corresponds to the items newly discovered, being either yet undiscovered or taken by other species. A colony of species i discovers food items at discovery rate D_i, and it can discover either yet undiscovered items, R, or items taken over by a colony of species j, R_j, with probability $C_{i,j}$. The second term of (3.1.b) corresponds to previously owned food items lost due to consumption or usurpation by colonies of other species. Controlled items R_i are harvested according to the exploitation rate E_i and can be usurped by colonies of species j with probability $C_{j,i}$ according to the discovery rate of the population j, D_j.

$$\left\{\begin{array}{lcll} \frac{dR}{dt_R} & = & \sigma_R - R\sum_{i\in[1,n]} q_i D_i & (3.1.a) \\ \frac{dR_i}{dt_R} & = & D_i(R+\sum_{j\in[1,n]-\{i\}} C_{i,j}q_jR_j) - R_i(E_i+\sum_{j\in[1,n]-\{i\}} C_{j,i}q_jD_j) \quad ,\forall i\in[1,n] & (3.1.b) \end{array}\right. \tag{3.1}$$

System (3.1) has a unique stable solution: R^* and $R_i^*, \forall i \in [1,n]$ (Existence, uniqueness and stability of this solution are proved in Appendix 3.5.A). Food item dynamics are much faster than ant colony population dynamics. Food items change daily, whereas the establishment of new colonies occurs at an annual time scale (Gordon, 1991). This difference in timescales allows us to consider that food items remain at their fluctuating stable equilibria, while the number of colonies oscillate. We can thus consider the number of items controlled by each colony as a function of foraging ability (D_i, E_i, and D_j, E_j, with $j \neq i$), colony number (q_i, and q_j, with $j \neq i$), and competitive interference between species ($C_{i,j}$ and $C_{j,i}$, with $j \neq i$).

The net rate of energy intake of a single colony of species i is given by the equilibrium number of food items this colony controls, R_i^*, times the exploitation rate of this species, E_i, and the amount of energy available per item, e_R (and assumption (ii) states $e_R = \sigma_R^{-1}$). This net rate of energy intake will be a key component of the fitness model (3.2).

The growth rate of a population of colonies depends on the amount of energy the colonies obtain (the net rate of energy intake), and the efficiency at which energy is converted into new colonies (σ_q). Let parameter γ be their mortality. The simplest differential equation describing the dynamics of population i is

$$\frac{dq_i}{dt} = q_i\left(\frac{\sigma_q}{\sigma_R} E_i R_i^* - \gamma\right) \tag{3.2}$$

From system (3.1), assuming a single species r, and that item dynamics have reached equilibrium ($R^* = \frac{\sigma_R}{q_r D_r}$, $R_r^* = \frac{\sigma_R}{q_r E_r}$), equation (3.2) becomes

$$\dot{q_r} = \sigma_q - q_r\gamma \tag{3.3}$$

Mutations are assumed to be rare enough to allow the population dynamics to stabilise before mutants appear. The resident species reaches its asymptotically stable equilibrium $q_r^* = \frac{\sigma_q}{\gamma}$ (equation (3.3)).

The evolutionary analysis consists in determining the dynamics of a resident-mutant community, with the resident species r initially at equilibrium q_r^*, and a mutant species s initially sparse. The resident-mutant system is deduced from equation (3.2) and system (3.1) with two populations r and s (cf. Appendix 3.5.B)

Will the mutant be able to establish itself in the community? Will it supplant the former resident? Will both species coexist? Will a coalition of two coexisting species resist invasion by a new mutant? The answers to these questions depend on the shape of the invasion fitness value (or invasion eigenvalue), which represents the per capita growth rate of an initially rare mutant in a community of residents: $\mathcal{F}_r(s)$ at the particular value $q_r = q_r^*$ and $q_s = 0$:

$$\mathcal{F}_r(s) = \gamma\left(\frac{D_s E_s(\sigma_q C_{s,r} D_r + \gamma E_r)}{D_r E_r(\sigma_q C_{r,s} D_r + \gamma E_s)} - 1\right) \tag{3.4}$$

The long-term evolution of the foraging strategy can be entirely predicted from $\mathcal{F}_r(s)$ (cf. equation (3.4)). Indeed, the slope of the invasion fitness at $s = r$ ($\frac{\partial \mathcal{F}_r(s)}{\partial s}|_{s=r}$), called the selection gradient, informs the direction and speed of evolutionary changes (Metz et al., 1996; Law et al., 1997). The values at which the selection gradient vanishes (the so-called evolutionary singular strategies, SS) are the equilibrium points of the evolutionary dynamics. SSs can be discriminated according to their evolutionary stability. When they are stable, no nearby mutants can invade the resident population, and the strategy constitutes an evolutionary stable strategy (ESS) (Maynard Smith, 1974). An SS is said to be convergence stable (CSS) when it acts as an evolutionary attractor: the strategies in the vicinity of the SS will evolve toward this point (Christiansen, 1991). The conditions for a foraging strategy to be SS, ESS and CSS in our model are listed in Appendix 3.5.C.

3.2.2 Foraging processes

To illustrate the trade-off between discovery, exploitation and interference competition, we need to describe explicitly the functions D_i, E_i, and $C_{i,j}$. We aim to establish simple functions that reflect the mechanisms implicated in the foraging processes (discovery, exploitation, and competition) making clear the contribution of both foraging strategy and food item dispersion.

The assumptions we made above reduce the complexity of the environment: Assumption (i) establishes that food items are randomly distributed with density ρ. From this statement, we deduce that the mean distance between the nest and the first item encountered is $\frac{1}{2\rho^{\frac{1}{2}}}$ (Moore, 1954) (Oster and Wilson, 1978). We will take this value as the mean distance between the nest and the items. According to assumption (ii), the size of food items is inversely proportional to their density. Let ρ^{-1} be the size of food item. Moreover, considering resources as two-dimensional items, we can then estimate that item diameter measures about $\rho^{-1/2}$.

Discovery rate (D_i) The discovery rate expresses the number of food items discovered by a colony per unit time. Between time t and $t + dt$, an individual forager (a scout) explores an area depending on its speed v, the time spent searching dt, and its perception of food sources (Pearce-Duvet and Feener, 2010). Assuming that the long-distance sensory acuity of ants is negligible (Gordon, 1995), ants perceive patches by contact. So, the maximum distance at which they would perceive a food item is that of a item diameter, i.e. $\rho^{-1/2}$. The simplest approximation of the area explored by a single scout is then $v\rho^{-\frac{1}{2}}dt$. Considering that the number of food items per unit area is ρ, the number of patches encountered by a single scout is $v\rho^{\frac{1}{2}}dt$. There are w workers in the colony of which $(1 - x_i)w$ are individual foragers. We consider there is no interference between searching foragers, so the overall search rate of the colony is $D_i = v\rho^{\frac{1}{2}}(1 - x_i)w$

In this approximation, we neglect that ants do not search in a straight path, but lose efficiency by searching multiple times the same area. This might become critical for low renewal rates.

Exploitation rate (E_i) The exploitation rate represents the fraction of each controlled item consumed per time period. We assume that individual foragers remember the position of the food item they exploit and are able to return to it after delivering a food load to the nest. There is always at least one ant harvesting an item. The other ants exploiting the item are those recruited among the x_iw potential recruits in a colony. We consider that all recruits are uniformly distributed across the different food items discovered. The number of food items discovered is D_i, and $\frac{x_i w}{D_i}$ is the number of available recruits for a single item. Nevertheless, the recruitment process does not involve all the potential recruits from the moment the resource is discovered: the ant trail allowing recruitment needs several depositing ants to be efficient. Therefore, the number of foragers involved in the foraging process depends on the number of trips needed to deplete the items: if the number of needed trips is large, making the trail efficient, $\frac{x_i w}{D_i}$ is a good approximation of the number of effective recruits per item; if the number of needed trips tends to zero, the number of effective recruits also tends to zero (the item is depleted before the recruitment process become efficient). The number of effective recruits per item can then be modelled by the asymptotic function $\frac{x_i w}{D_i}(1 - \frac{1}{\text{nb. of needed trips}})$. The number of trips needed to deplete an item is inversely proportional to the loading capacity of ants l. Assuming that the size of items is proportional to ρ^{-1}, the food source is depleted with $\frac{\rho^{-1}}{l}$ trips. To sum up, there are $1 + \frac{x_i w}{D_i}(1 - \rho l)$ ants harvesting a single item: the ant that discovered the item and kept harvesting it, and the number of effective recruits. There are thus $1 + \frac{x_i}{v\rho^{\frac{1}{2}}(1-x_i)}(1 - \rho l)$ ants exploiting each controlled item.

The mean distance between a patch and the nest is $\frac{1}{2\rho^{\frac{1}{2}}}$. Consequently, ants feeding at a food item spend $\frac{1}{v\rho^{\frac{1}{2}}}$ time for a round trip (ie twice the distance). A harvesting ant brings to the nest a load $lv\rho^{\frac{1}{2}}$ per unit time. The colony exploitation rate is then $E_i = lv\rho^{\frac{1}{2}}(1 + \frac{x_i}{v\rho^{\frac{1}{2}}(1-x_i)}(1 - \rho l))$. This expression matches intuitive inferences about the harvesting process: 1/ The more the colony recruits, the faster it exploits food items. 2/ The higher the density of resources, the less sensitive exploitation efficiency is to foraging strategies. This is true because as item size becomes smaller, so does the advantage of mass recruitment; the smallest items would be most efficiently gathered by a single ant.

Competition ($C_{i,j}$) To emphasize the importance of competition in ant communities, we will consider two different kinds of communities. The first one is a “first come, first served” community: once a colony has discovered a food item, it cannot be dislodged by another colony ($C_{i,j} = C_{j,i} = 0$). In the second community, colonies compete for food items and a colony of species i usurps a food item from a colony of species j with probability $C_{i,j}$.

Adler et al. (2007) considered a dominance-discovery trade-off and assumed that a species with a higher discovery rate was unable to dislodge a species with a lower discovery rate. However, these authors do not explicit the mechanisms leading to this trade-off. We consider that the probability to win a contest (and usurp the item) depends on the number of workers actively involved in harvesting the item. The greater the difference between the number of ants of colony i and colony j at a food item, the higher the probability that the colony of species i will outcompete the colony of species j. In particular, if the number of workers of two colonies competing for an item is the same, both colonies will have the same probability of winning the item: $\frac{1}{2}$.

As we previously established, a colony with foraging strategy x_i involves $1 + \frac{x_i}{v\rho^{\frac{1}{2}}(1-x_i)}(1-\rho l)$ workers harvesting a single food item. The difference between the "work forces" of i and j is then $S_{i,j} = \frac{(1-\rho l)}{v\rho^{\frac{1}{2}}}(\frac{x_i}{(1-x_i)} - \frac{x_j}{(1-x_j)})$. We modulate this difference $S_{i,j}$ by a coefficient ϕ that indicates the intensity of competition. If $\phi = 0$, the competition is symmetric and all colonies have the same probability $\frac{1}{2}$ of winning the item whatever their foraging strategies. The higher is ϕ, the stronger is the asymmetry and higher is the impact of workforces difference. To model competition, we use the following phenotypical function $\frac{1}{1+e^{-\phi S_{i,j}}}$. This function fulfils the requirements of competitive symmetry when $\phi = 0$ and when two populations use the same foraging strategy. Moreover, when $\phi \neq 0$, the difference between the discovery rates of colonies i and j is greater with i being faster than j, and thus the greater the probability that i will dislodge j. Therefore, the function $C_{i,j} = \frac{1}{1+e^{-\frac{\phi(1-\rho l)}{v\rho^{\frac{1}{2}}}(\frac{x_i}{(1-x_i)} - \frac{x_j}{(1-x_j)})}}$ is in agreement with Adler's intuition on interference competition.

3.3 Results

The resident-model we defined in the previous section enables two sorts of analyses: a classical approach of population dynamics, and predictions on the long term evolution of foraging strategies. In our work, population dynamics explains the possible coexistence of two species with different foraging strategies, assuming that these species have already settled in the community. Furthermore, long-term evolution, assuming a single initial strategy, determines which strategy will be selected in the long run. In this section, we show that both approaches lead to complementary results that highlight the importance of competition in ant communities.

3.3.1 Species coexistence

First, we study the conditions that allow the coexistence of two species using individual foraging and mass recruitment respectively. We analyse three types of communities differing in characteristics of competition: a "first come, first served" community, and communities where competition is respectively symmetric or asymmetric. In the first type, a colony can never usurp a food patch discovered by another colony ($C_{i,j} = C_{j,i} = 0$). In the second one, each colony has the same probability of usurping a food patch from another colony, regardless of their respective foraging strategies ($C_{i,j} = C_{j,i} = \frac{1}{2}$). In the third type, the probability of winning a food patch depends on the foraging strategy employed and on the environment (see previous section for the expression of $C_{i,j}$).

The resident-mutant model suggests that in a "first come, first served" community, the coexistence of two species using different foraging strategies is never possible (Appendix 3.5.B). The species with the higher discovery rate will persist, and the other vanishes. This is shown in Fig. 3.2 A where only the individual foraging species has a non null number of colonies, whereas the mass recruiting species reaches 0 as stable equilibrium. In an environment where no usurpation is possible, the best strategy would be to maximise the discovery rate, investing preferentially in the number of individual foragers (or scouts). As a consequence, in this type of community, individual foraging species take over the community independently of the environment.

In a community where colonies compete for resources, coexistence is possible (Appendix 3.5.B). The coexistence of both species relies on the interplay between discovery rates, exploitation rates, and usurpation probabilities. In the case of symmetric competition, this coexistence strongly depends on the characteristics of the environment. Food item size and density determine the relative gain of both species according to their discovery and exploitation rates. If food items are relatively large, the two species coexist: both discovery and exploitation are stable strategies. However, if food items are small, it is not worth investing in exploitation, because the advantage won is lower and only the individually foraging species persists. As illustrated in Fig. 3.2 B, if food items are sparse and therefore large ($\rho \leq 0.3$ in Fig. 3.2 B), both species coexist; if food items density is higher and items are smaller ($\rho > 0.3$ in Fig. 3.2 B), only the individually foraging species persists.

In the case of asymmetric competition, both populations may always coexist. Investing in collective foraging (recruitment) gives an additional advantage by increasing the probability of usurping patches from other colonies. The two strategies, fast discovery, slow exploitation and weak competitive ability on the one hand, and, on the other, slow discovery, fast exploitation and strong competitive ability, can cohabit. The stability of coexistence is independent of the density of food items, except for the limiting case $\rho = 1$ that means that a single foraging ant can carry each food item in one load. In this case, only the individually foraging species would persists. Additionally, the number of colonies at equilibrium is independent of the density of food patches (Fig. 3.2 C), and the number of colonies of the individually foraging species at equilibrium is lower than that of the mass recruiting species (10 colonies for the individual foraging species and 90 colonies for the mass recruiting species in Fig. 3.2 C).

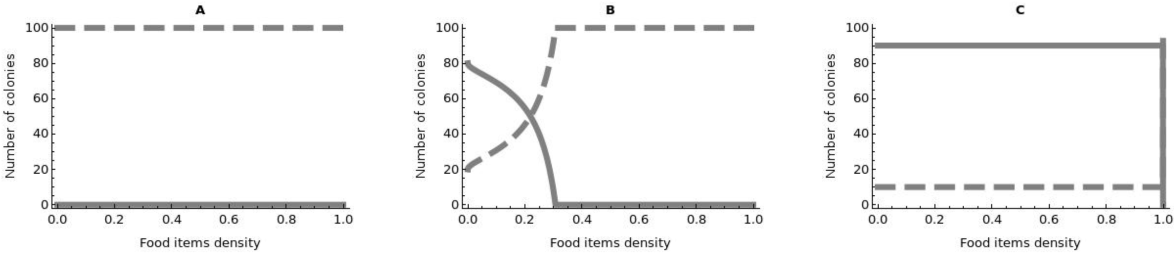


Figure 3.2 — The number of colonies at equilibrium of two species using respectively individual foraging strategy ($x_i = 0$) in dashed lines, and mass recruitment ($x_j = 0.9999$) in full lines, as a function of the density of food patches. A, "first come, first served" community: the probability of usurping a food item is null. B, symmetric competition: the probability of usurping a food item is $\frac{1}{2}$, independently of the species. C, asymmetric competition: the outcomes of interference competition depends on the species (asymmetry strength $\phi = 1$), see text for details about $\rho = 1$. Other parameters $w = 1000, \sigma_q = 0.1, \gamma = 0.001, v = 1, l = 1$.

Depending on the qualitative behaviour of the species, we can divide the environment into two categories: environments where food items are sparse and large; and environments where food item density is high and items small. Whatever the community or the environment, the individually foraging species persists. The mass-recruiting species persists (therefore coexists with the individual foraging species) only if the community is submitted to interference competition. If competition is symmetric, mass recruitment only persists in an environment with sparse and large food items. If the competition is asymmetric, it persists for all kinds of food items (provided that they are larger than what a single foraging ant can carry). Table 3.3 summarises all these results.

Table 3.3 — Possible coexistence between individual forager and mass recruiter species

	RESOURCE CHARACTERISTICS	
	Few large items	Many small items
COMPETITION		
None	no	no
Symmetric	yes	no
Asymmetric	yes	yes

3.3.2 Long term strategy evolution

We consider an ant community evolving through mutation/selection processes, from an ancestor community in which all colonies use the same foraging strategy. Using an adaptive dynamics approach (Dieckmann and Law, 1996; Metz et al., 1996), we study the evolutionary dynamics of foraging strategies, and show how the community is shaped by the interplay between competition and food item density. Two key questions we seek to answer are: i/ Which foraging strategy will be selected in different environments? ii/ Will several distinct strategies emerge and coexist? The answer to these questions hinges on the analysis of the singular strategies (i.e. the strategies for which the fitness gradient vanishes).

In a “first come, first served” community, there are no interference interactions ($C_{i,j} = C_{j,i} = 0$): the first colony discovering a food item controls it. The analysis of singular strategies shows (Appendix 3.5.C) that evolution will select the strategies that maximize the discovery process. Indeed, in singular strategies, the derivative of the discovery rate vanishes ($D'_r = 0$). In addition, the conditions for both evolutionary stability and convergence stability are identical. As a consequence, if the strategy is a maximum of the discovery rate ($D''_r < 0$), it is both stable and convergence stable; if the strategy is a minimum of the discovery rate ($D''_r > 0$), it is neither stable nor convergence stable. There cannot be an emergence of polymorphism in this community: whatever the initial conditions, evolution leads towards a single strategy. This “ending point” is the strategy that maximizes patch discovery. When we consider the foraging process as specified in the previous section, there are no singular strategies sensu stricto (there is no $r \in [0, 1]$ such as $D'_r = 0$). However, the whole system converges toward the individual foraging strategy ($x_r = 0$) that optimizes the patch discovery process within the range of biologically meaningful traits ($x_r \in [0, 1]$), and stops there (no mutants can invade). Individual foraging ($x_r = 0$) is the only evolutionary and convergent strategy, independently of the environmental characteristics (i.e. resource density). A community characterised by the “first come, first served” principle would lead to the establishment of an individual foraging species.

In a community where species are subjected to competition, several evolutionary scenarios might occur depending on the characteristics of the discovery rate, the exploitation rate, and the probability of usurping food items (D_i, E_i, and $C_{i,j}$). These scenarios are analyzed considering these functions as specified in the previous section. Some parameters that are identical for all populations have been arbitrarily fixed. The ant loading capacity (l) has been fixed so that only the smallest food items might be carried by a single ant in one load. As the smallest item size (ρ^{-1}) is 1, we fixed l as unity. As neither space nor time is explicitly considered in the patch dynamics, we can consider ant speed (v) as unity without loss of generality. Notwithstanding, we checked that a variation of 10 % of the parameter value did not change the results significantly. We consider that each colony has 1000 foragers. To make sure this value was not critical for qualitative results, we ran out analyses with colony sizes ranging from 100 to 10000 foragers (this range covers most ant species (Beckers et al., 1989)). The results are qualitatively robust, and quantitative changes in estimations are less than

10^{-2}. The estimation of the efficiency of energy reconversion into new colonies σ_q and colony mortality rates γ have been arbitrarily fixed to 0.1 and 0.001. The results are qualitatively robust provided that the ratio $\frac{\gamma}{\sigma_q}$ remains finite (i.e. γ is either smaller or about the same order of magnitude than σ_q). Qualitatively, the results show that evolutionary dynamics are independent of the particular value of these parameters: the same conclusions would be valid for different values of these parameters. However, both food item density and the strength of competition asymmetry influence the long term evolution of foraging strategies. The changes in the qualitative structure of strategy evolution are studied as a function of food item density (parameter ρ). We highlight the interplay between this bifurcation parameter and the strength in competition asymmetry (parameter ϕ).

When food items are scarce and large ($\rho < 0.382$ in Fig. 3.4), there is a unique singular strategy, both evolutionarily and convergence stable: invest largely in recruits. The exact value of the evolutionarily stable proportion of recruits depends somewhat on the type of competition: $x_r = 0.85$ for symmetric competition (Fig. 3.4 A) and $x_r = 0.99$ with strong asymmetric competition (Fig. 3.4 D). The overall qualitative behaviour remains unchanged: the optimal strategy is mass recruitment. This result is quite intuitive: even if a colony with few scouts is less efficient in discovering resources, if the food items are large enough, it is worth investing in recruitment to efficiently exploit the large food items. Besides, the optimal proportion of recruits x_r if competition is asymmetric and competitive ability increases with the number of recruits. Indeed, if competition is symmetric, a higher proportion of recruits boosts the exploitation rate, but has no influence on the competitive ability (probability of controlling the food items). Conversely, a greater asymmetry in competition implies that both the exploitation rate and the probability of maintaining control of food items increases with the proportion of recruits. In this latter case, the optimal investment in recruits is higher.

The bifurcation value ($\rho_1 \approx 0.382$) is independent of the kind of competition. However the evolutionary dynamics when patches are more abundant and smaller ($\rho > 0.382$) differ with the symmetry of competition. There is a gradient of evolutionary behaviour between symmetric and strongly asymmetric communities that can be summarised into four types: symmetry, weak asymmetry, medium asymmetry and strong asymmetry.

For symmetric competition, for a density of food items higher than the bifurcation value, there is no singular strategy sensu stricto. However, as we found in the case without competition, long term dynamics converges toward the individual foraging strategy ($x_r = 0$) that is evolutionary stable. Evolution leads then to a single individual foraging population (Fig. 3.4 A).

In a community where competition is weakly asymmetric, a second bifurcation appears:

$\rho_2 \approx 0.47$ when $\phi = 0.001$ (Fig. 3.4 B). For intermediate patch densities ($\rho_1 < \rho < \rho_2$), a "repellor" singular strategy (neither evolutionary nor convergence stable) divides the evolutionary processes depending on the initial conditions (the strategy of the first ancestor). Evolution leads either toward an individual foraging strategy, or towards a branching point. If the initial proportion of recruits is lower than the repellor value, an individual foraging strategy will be selected. If the initial strategy is higher than the repellor, the strategies progressively increase until reaching a branching point. This singular strategy is an attractor of directional evolution (convergence stable) but lacks evolutionary stability (mutants might invade). Evolution leads the strategy towards the singular strategy, but once reached, it cannot stop there. Disruptive selection gives rise to a dimorphism, and the two strategies diverge. However, after a branching event occurs, when the population has become dimorphic, evolution might proceed according to several scenarios: either the population remains dimorphic, or becomes again monomorphic, or even reaches a higher level of polymorphism. We will focus on this event further on. For higher patch densities ($\rho_2 < \rho$), the dynamics is the same as in the symmetric case, i.e. the individual strategy is selected (Fig. 3.4 B).

In the case of medium asymmetry, the second bifurcation value (ρ_2) tends to 1 (Fig. 3.4 C). Actually, ρ_2 increases with the asymmetry value (ϕ). However a third bifurcation appears: $\rho_3 \approx 0.41$ when $\phi = 0.1$ (Fig. 3.4 C). For intermediate patch densities ($\rho_1 < \rho < \rho_3$), the repellor singular strategy disappears, leaving the branching point. In this case, independently of the initial conditions, evolution leads to a dimorphism of stable strategies. For higher patch densities ($\rho_3 < \rho$), the dynamics remains identical to those of the weak asymmetric case when $\rho_1 < \rho < \rho_2$. According to the initial strategy, evolution leads either toward individual foraging, or towards a dimorphism in which the two opposing strategies coexist.

For strong asymmetry, the third bifurcation value (ρ_3) tends to 1^-: ρ_3 also increases with the asymmetry value (ϕ), and for strong asymmetry ($\phi = 10$), $\rho_3 \approx 0.92$ (Fig. 3.4 D). The dynamics remain identical to those in the medium asymmetric case. Note that the range of densities leading to the evolution of dimorphism in strategies ($\rho_1 < \rho < \rho_3$) expands.

The combined influence of patch density and competitive asymmetry in the evolutionary dynamics is thus decisive when the community is subjected to competition. When patches are scarce and large, mass recruitment will be selected. If competition is symmetric, rising patch density (and therefore diminishing patch size) selects for individual foraging strategy. However, increasing competition asymmetry expands the conditions that induce the emergence of polymorphism. When parameter $\rho = 1$, individual foraging will be selected independently of the competition.

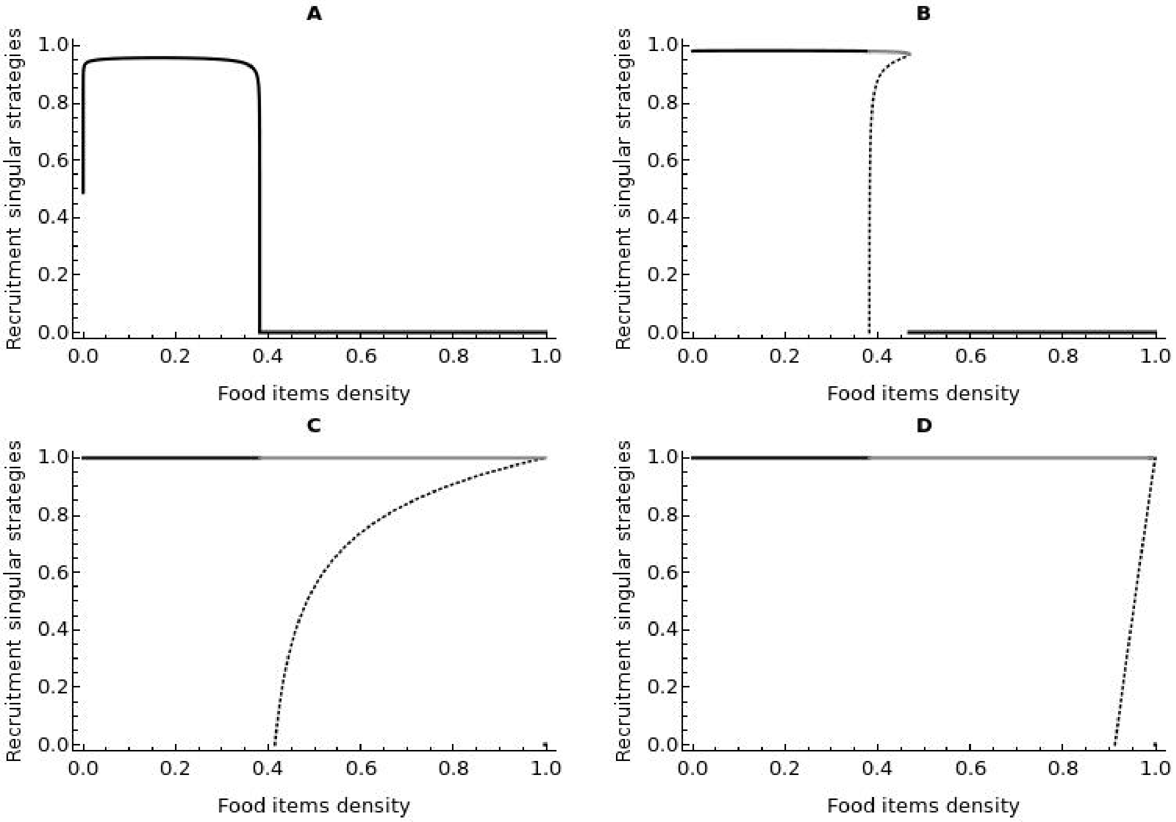


Figure 3.4 — Bifurcation diagrams representing the singular strategies x_r (proportion of recruits within colonies) and their stability properties as a function of the food items density. Black thick lines stand for Ending points (evolutionary and convergence stable), Black dashed lines stand for Repellors (evolutionary and convergence unstable), and gray thick lines represent Branching points (evolutionary unstable and convergence stable). The values and status of the singular strategies are plotted for different kinds of communities: A, a community submitted to symmetric competition ($\phi = 0$); B, a community submitted to weak asymmetric competition ($\phi = 0.001$); C, a community submitted to medium asymmetric competition ($\phi = 0.1$); D, a community submitted to strong asymmetric competition ($\phi = 10$). Parameters have been set to $w = 1000, \sigma_q = 0.1, \gamma = 0.001, v = 1, l = 1$.

The adaptive dynamics framework allows us to identify the mechanisms leading to the emergence and subsistence of a diversity of strategies. Strategy polymorphisms appear when a branching event occurs. However, further analysis is needed to clarify the full evolutionary scenario. Once dimorphism appears, the community is composed of two resident populations (or species), each characterised by their specific strategy. Mutations might occur in both populations, and a mutant might either replace one of the resident populations (conserving dimorphism), both residents (with loss of dimorphism), or establish as a third resident population (higher diversity). The evolution of the community depends on the invasion fitness of a scarce mutant in the dimorphic resident community (Geritz et al., 1999). As the singular strategies in the monomorphic case, the singular coalitions are the rest points of evolution in a dimorphic resident community. In our model, there is no singular coalition in the range of biologically meaningful traits. The evolution of strategies once the community becomes dimorphic is strongly stochastic. However, a graphical analysis of evolutionary isoclines (Appendix 3.5.D) suggests that in most cases, once the branching point is reached, the community remains dimorphic, and quickly evolves toward an equilibrium. If the strength of asymmetry in competition is weak, individual foraging and mass recruitment (x_{r_1} = 0, and x_{r_2} reaching nearly 1) will form a coalition as illustrated in Fig. 3.5 A. If the asymmetry is higher, the outcomes are more variable, and different equilibria might emerge as shown in Fig. 3.5 B and Fig. 3.5 C for identical conditions (see Appendix 3.5.D for explanations).

To further explore how evolution proceeds, we performed simulations integrating stochastic mutation processes (see Fig. 3.5). We consider a resident community initially composed of a single population at equilibrium q_r. At each time step, a mutant is generated (the mutant strategy is an aleatory variable normally distributed with the resident strategy as mean and a given genetic variance). If the mutant can invade the community, the stable equilibrium of the resident-mutant system is estimated. If the number of colonies of the resident population does not reach a stable non-trivial equilibrium, the resident vanishes and the mutant strategy becomes resident. If both resident and mutant populations reach a stable non trivial equilibrium, they constitute the new resident dimorphic community. When the community is composed of several resident populations, one of the strategies is randomly chosen to generate a mutant (a single mutant is generated at each time step). The analysis of residents-mutant system specifies whether the mutant, or one of the resident populations vanishes, and estimates the stable equilibrium number of colonies for each population. In these simulations, no more than four populations may be maintained in the resident community.

The simulations of Fig. 3.5 show the emergence of polymorphism once the branching point is reached. Note that when the monomorphic evolutionary dynamics do not reveal the existence of a repellor point, all ancestral strategies lead to the emergence of dimorphism (as shown in Fig. 3.5 B-C with individual foraging as ancestor strategy). If a repellor point is present, to lead to dimorphism, the ancestor strategy must be higher than the repellor value (as shown in Fig. 3.5 A with mass recruitment as ancestor strategy). All the evolutionary trees illustrated by the simulations highlight that the dimorphic community keeps co-evolving until reaching an equilibrium (provided that the stochasticity of mutation processes allows such variation).

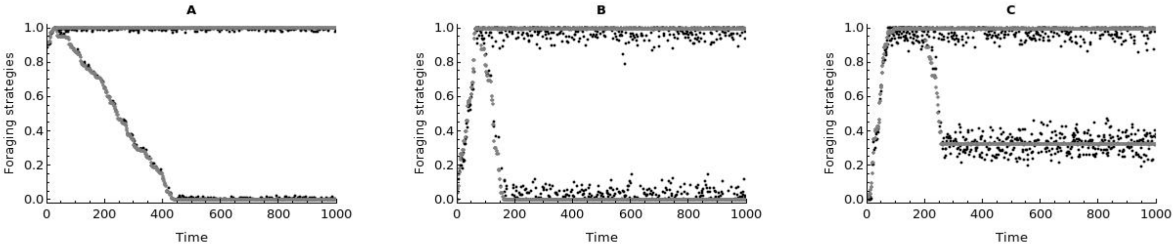


Figure 3.5 — Simulated evolutionary trees of foraging strategies that illustrate the emergence and persistence of polymorphism in the community. A, the ancestor strategy is mass recruitment ($x_r(0) = 0.9$), food items density is $\rho = 0.5$, asymmetric competition is parametrized with $\phi = 0.01$, and genetic variance is 0.01. B-C, the ancestor strategy is individual foraging ($x_r(0) = 0$), food items density is $\rho = 0.4$, asymmetric competition is $\phi = 0.1$, and genetic variance is 0.05. Other parameters have been set to $w = 1000, \sigma_q = 0.1, \gamma = 0.001, v = 1, l = 1$.

In this section, we showed that, despite the simplicity of the mechanisms described in the model, we can explain the emergence and persistence of diverse foraging strategies in ant communities. Indeed the explicit trade-off between discovery and control / exploitation of the patches allows strategy diversity, despite the strong assumption that the environment is made of a single type of resource. We can split the environments into two categories according to food patches being either sparse and large or dense and small. Table 3.6 summarises the strategies that are selected in the two environments according to competition type.

Table 3.6 — Evolution of foraging strategies

	RESOURCE CHARACTERISTICS	
	Few large items	Many small items
COMPETITION		
None	individual	individual
Symmetric	mass recruitment	individual
Asymmetric	mass recruitment	diversity of foraging strategies

3.4 Discussion

We model the evolutionary dynamics of foraging strategies from the competitive interspecific relations within the community. Assuming a distinction between scouts and recruits within the foragers of a colony, we characterize the foraging strategy as the proportion of foragers that are recruits. This trait is involved in a double trade-off between resource discovery, and both resource exploitation and dominance. We present a model of foraging processes (including resources discovery, exploitation, and interference competition) that explicitely takes into account the mechanisms underlying these trade-offs: i/ The more a species invests into scouts, the faster it discovers resources; ii/ The higher the number of foragers involved in the recruitment process, the faster is the exploitation of resources; iii/ In case of the co-occurrence of two colonies of different species on a single resource, the outcome of interference competition depends on the form of competition. We consider three cases. 1/ a "first come, first served" community, where the first species to discover a resource patch monopolises it. It could also be considered as a case of strong preemptive competition (Schoener, 1983), even though this concept is more adequate to space occupation than the control of food items. In spite of its heuristic interest, this case seems quite unrealistic in ant communities where the first species to discover resources is often driven away by more dominant species (Fellers, 1987; Holway, 1999). For this kind of community, individual foraging strategy is the unique Evolutionary Stable Strategy. No other foraging strategy could coexist with the individual strategy in a community in the absence of interference competition. The two other kinds of competition we consider are: 2/ Symmetric competition: all colonies have the same chance to drive away a co-occurring colony, regardless of their respective foraging strategies; and 3/ Asymmetric competition: when two colonies compete for the same food source, the most likely winner is the species that engages more recruits. The strength of asymmetry controls the advantage gained by the species with more recruits.

When analyzed with a classical population dynamics approach, our results support Adler et al. (2007) suggestion that the dominance-discovery trade-off could maintain the diversity in ant communities. We have shown that, in a community subjected to strong asymmetric competition, a mass recruiting species can coexist with an individual foraging species independently of the size and density of resources. However, when relaxing the assumption of asymmetric competition, the outcome depends on the type of food items. In a community subjected to symmetric competition, if resources are scarce and large, both collective foraging species and individual recruiting species can coexist, whereas if food items are small and at high density, collective foraging species extinguish, and the unique foraging strategy maintained is individual foraging.

The adaptive dynamics framework provides an evolutionary approach that shows how strategy diversity is generated and maintained. Asymmetric interference competition is required for the evolution of a single strategy into two coexisting strategies. The dominance-discovery trade-off does not only maintain diversity, but also creates it. In communities with symmetric interference competition, evolution leads to the establishment of a single species. This species use either individual or collective strategies depending on the density and size of resource patches. The stronger the asymmetry, the wider the range of environmental conditions that leads to a diversification of foraging strategies. The ancestral strategies evolve by directional selection toward a fitness minimum, and disruptive selection causes an adaptative splitting of strategies, leading to species specialisation on two different foraging strategies.

The emergence of diversity might depend on the ancestral strategy. With weak asymmetric competition, the evolutionary dynamics would lead to a polymorphism of strategies only if the evolutionary process starts from a collective strategy. Conversely, with strong asymmetric competition, diversity would emerge independently of the ancestral characteristics. Note that in all cases, branching only occurs for high values or x_r, so if the ancestral strategy were individual foraging, it would have first to evolve to mass recruitment before polymorphism could emerge. Our prediction makes obsolete the classical classification of individual foraging species as primitive. Indeed, even if our model does not generate suggestions on which was the first ancestor foraging strategy, it predicts that the actual individual foraging species derive likely from collective foraging ancestors. Ruano et al. (2000) present results supporting the suggestion that environmental conditions induced the establishment of the different foraging strategies used by ant species.

Our model suggests that interference competition is crucial to explain the diversity in ant strategies. Interestingly, the results hint that evolution might favor the apparition of both dominant, mass recruiting, species and submissive, individual foraging, species in a single process. This prediction is in contrast with the hypothesis that submissive species are "suboptimal" species whose coexistence with dominants is allowed by the occupation of suboptimal niches (Tanner and Adler, 2009). Indeed, as shown by Adler et al. (2007), submissive species jeopardize the persistence of competitive dominants by imposing to dominants a minimum discovery rate below which they would be excluded. Actually, the predictions of this model are in contrast with the assumptions of either the lack of influence of submissive species on the competitive dominant or the evolution of dominance as a strategy to take over food from discoverers. This work suggests that both strategies are evolutionary stable, and that the specialisation of feeding habits and strategies in the community is the result of species coevolution within the community.

Our work suggests that simple trade-offs can lead to a diversification of strategies through evolutionary branching. Throughout this study, we defined a set of colonies that share the same foraging strategy as a species. Notwithstanding, branching events do not necessarily imply speciation but rather make sympatric speciation possible (Geritz et al., 2004). The real outcome of disruptive selection due to evolutionary branching might vary from speciation to phenotypic plasticity (Rueffler et al., 2006). Nevertheless, local processes initiated by phenotypic plasticity might give rise to alternative specialisation, and sympatric speciation via polymodal selection (West-Eberhard, 1986). Our model is far too simplistic to be a solid base to explore speciation in ant species. Notwithstanding, it contributes to the understanding of foraging strategies and suggests that phenotypic variation is promoted by frequency-dependence mechanisms. Neither geographical patterns, nor complex environments are required to explain diversity.

In our model, the frequency-dependence effect depends on a parameter representing the intensity of the trade-off between resource discovery and dominance. This trade-off is known to be subjected to different selective pressures in ant communities. First, the abiotic conditions such as temperature might have an influence on the outcome of interference competition (Cerdá et al., 1998c; Bestelmeyer, 2000). Second, specific predators such as parasitoid flies seem to affect community structure (Feener, 2000; Lebrun, 2005; Lebrun and Feener, 2007). Experimental work shows that parasitoids are attracted to the pheromones of their hosts (Feener et al., 1996). The trail pheromone laid by recruiting ants could be used as olfactory cues by parasitoids to locate their hosts. This mechanism would induce a positive correlation between collective foraging behaviour and vulnerability to specific parasitoids. Both theoretical and empirical evidence highlights that the trade-off between recruitment and vulnerability to parasitoids reinforces the dominance-discovery trade-off (Lebrun and Feener, 2007). The so-called "balance of terror" might be determinant in shaping the asymmetry of the competition in natural communities (Adler, 1999).

This study joins with many theoretical predictions in underlining the importance of trade-offs in reducing competitive exclusion. Negative interactions between life history traits might occur at different spatial scales, and involve many different functions (see Kneitel and Chase (2004) for review). The trade-offs involved in our model are not specifics to ants: their role in community diversity have been discussed in many theoretical studies. First, the interference-exploitation trade-off seems to allow consumer species coexistence, regardless of the dynamics of resources (Amarasekare, 2002). Then, the dominance-discovery trade-off oppose competitive abilities versus food source colonization capacities as in the classic competition-colonization trade-off. The latter is known to promote species coexistence (Tilman, 1994) even when relaxing the intensity of the competitive trade-off (Calcagno et al., 2006). The interaction between competitive trade-offs, local dispersal, and species-specific enemies is a mechanism maintaining coexistence in sessile organisms (Chave et al., 2002). Moreover, in frequency-dependent selection frameworks, trade-off shape is crucial for the evolution of life history traits (de Mazancourt and Dieckmann, 2004). It seems thus fundamental to understand the allocation constraints that give rise to such conflicts

(Amarasekare et al., 2004).

Our model fails to explain the full range of foraging strategies in ants. We consider only the case where two species coexist while exploiting a single and common resource. A more spatially heterogeneous environment would probably allow a higher degree of diversity, especially for small animals like ants (Hutchinson, 1959). More detailed models that take into account a more complex environment, would probably explain a wider range of foraging strategies.

In addition to the number and the quality of resources, this model could be extended in several other directions. Ant colonies are known to adjust task allocation according to both internal and external factors (Gordon, 1996). In particular, species able to handle collective foraging behaviour can efficiently match the efforts to the challenge of a variable environment according to resource distribution (Bernstein, 1975), size (Cerdá et al., 2009) and quality (Detrain and Deneubourg, 2002), and to the composition of the community (Putyatina, 2007). Mathematical models show that the behavioural flexibility of generalist species expands the conditions of coexistence of specialist and generalist species in the community (Abrams, 2006b,a). The fact that ant species can adjust their foraging strategies might also contribute to species diversity.

An important limitation of our model concerns the number of foragers in each colony. We considered the colony size as a constant and as a shared characteristic between all populations. Nevertheless, in ants, the demography of populations depends closely on the interactions of single ants with their environment. There might be a strong relationship between foraging strategy and colony size (Beckers et al., 1989). As the interacting units are the workers, their number is a key parameter in the population growth rate. In spite of this, further analysis has revealed that our model is not sensitive to this parameter, although a minimum number of workers is required to improve the fitness of the colony by recruitment foraging (Sumpter and Pratt, 2003). In a forthcoming paper, we aim to show that this relationship is not the cause, but the consequence of strategy optimality.

The present study designates asymmetric competition as the cornerstone of social foraging strategy diversity in ants. The novelty of our model is that it links microscopic processes, such as the mechanisms underlying the discovery and exploitation of food resources by a colony, to macroscopic evolution at the community level. This approach allows us to assess the evolutionary dynamics of recruitment strategies, and to identify the influence of such underpinning factors as resource size and density as well as interspecific competition.

Acknowledgements

We thank Jessica Pearce-Duvet, Claus Rueffler, Nate Sanders, Perrine Pelosse, Isabelle Amat and Manu Desouhant for early reviews and useful comments. Warm thanks are addressed to Laurent Gueguen for checking Appendix 3.5.A.

3.5 Appendix

3.5.A Patch dynamics stability

The equilibrium points of linear system (3.1) are the solutions of equation (3.5).

$$MX = B \tag{3.5}$$

$$\text{with } B = \begin{pmatrix} \sigma_R \\ 0 \\ \dots \\ 0 \end{pmatrix}, \text{ and}$$

$$M = \begin{pmatrix} -\sum_{i\in[1,n]} q_i D_i & 0 & 0 & \dots & 0 \\ D_1 & -(E_1 + \sum_{j\in[2,n]} C_{j,1} q_j D_j) & C_{1,2} q_2 D_1 & \dots & C_{1,n} q_n D_1 \\ \dots & & & & \\ D_n & C_{n,1} q_1 D_n & C_{n,2} q_2 D_n & \dots & -(E_n + \sum_{j\in[1,n-1]} C_{j,n} q_j D_j) \end{pmatrix}$$

A necessary and sufficient condition for the linear system (3.1) to admit a unique and stable solution is that all the elements of M's spectrum have a strictly negative real part.

$\lambda_0 = -\sum_{i\in[1,n]} q_i D_i$ is a trivial eigenvalue of M. We assume that there is at least one colony able to discover resources in the environment (ie $\exists i$ such as $q_i D_i \neq 0$). λ_0 is then a strictly negative real eigenvalue.

Let us now demonstrate that the eigenvalues of a matrix A_n all have a strictly negative real part. We define A_n according to coefficients $e_i > 0$, $a_{i,j} \geq 0$, and $q_i \geq 0$.

$$A_n = \begin{pmatrix} -(e_1 + \sum_{j\in[2,n]} a_{j,1} q_j) & a_{1,2} q_2 & \dots & a_{1,n} q_n \\ \dots & & & \\ a_{n,1} q_1 & a_{n,2} q_2 & \dots & -(e_n + \sum_{j\in[1,n-1]} a_{j,n} q_j) \end{pmatrix}$$

Note that if $\exists I \neq \{\}$ such as $\forall i \in I, q_i = 0$, then $\lambda_i = -(e_i + \sum_{j\neq i} a_{j,i} q_j)$ are strictly negative eigenvalues ($\forall i \in I$), and the remaining eigenvalues are those of a matrix $A_{n-card(I)}$.

Let us now show the stability of a matrix A_n with $q_i \neq 0, \forall i \in [1,n]$. As $q_i \neq 0, \forall i \in [1,n]$, the following transformations ($Row_i \leftarrow q_i Row_i$, and $Column_i \leftarrow \frac{Column_i}{q_i}$) conserve the eigenvalues.

Demonstrating that the spectrum of a matrix has strictly negative real parts is equivalent to proving that the spectrum of its opposite matrix has strictly positive real parts. Moreover, as a matrix and its transposed have the same eigenvalues, the real part of all the eigenvalues of B_n are strictly positive.

$$B_n = \begin{pmatrix} e_1 + \sum_{j\in[2,n]} a_{j,1}q_j & -a_{2,1}q_2 & \dots & -a_{n,1}q_n \\ \dots & & & \\ -a_{1,n}q_1 & -a_{2,n}q_2 & \dots & e_n + \sum_{j\in[1,n-1]} a_{j,n}q_j \end{pmatrix}$$

Let λ be an eigenvalue of B_n. There exists an eigenvector $X_n \neq 0$ such as $B_nX_n = \lambda X_n$. This equation is equivalent to the following system $\forall i \in [1,n]$:

$$\left\{ \begin{array}{lcl} (e_i + \sum_{j\neq i} a_{j,i}q_j)Re[x_i] - \sum_{j\neq i} a_{j,i}q_jRe[x_j] & = & Re[\lambda]Re[x_i] - Im[\lambda]Im[x_i] \\ (e_i + \sum_{j\neq i} a_{j,i}q_j)Im[x_i] - \sum_{j\neq i} a_{j,i}q_jIm[x_j] & = & Re[\lambda]Im[x_i] + Im[\lambda]Re[x_i] \end{array} \right. \tag{3.6}$$

Summing both rows of system (3.6) respectively multiplied by $Re[x_i]$ and $Im[x_i]$, we deduce:

$$\begin{aligned} (e_i + \textstyle\sum_{j\neq i} a_{j,i}q_j)(Re[x_i]^2 + Im[x_i]^2) - Re[x_i]\textstyle\sum_{j\neq i} a_{j,i}q_jRe[x_j] - Im[x_i]\textstyle\sum_{j\neq i} a_{j,i}q_jIm[x_j] \\ = Re[\lambda](Re[x_i]^2 + Im[x_i]^2) \end{aligned} \tag{3.7}$$

Equality (3.7) is true $\forall i \in [1,n]$. Let i be such as $(Re[x_i]^2 + Im[x_i]^2) = Max_{j\in[1,n]}(Re[x_j]^2 + Im[x_j]^2)$. Note that as X_n is an eigenvector, $(Re[x_i]^2 + Im[x_i]^2) > 0$. Follows:

$$Re[\lambda] = e_i + \sum_{j\neq i} a_{j,i}q_j(1 - \frac{Re[x_i]Re[x_j] + Im[x_i]Im[x_j]}{Re[x_i]^2 + Im[x_i]^2}) \tag{3.8}$$

We define two real vectors $V_i = \begin{pmatrix} Re[x_i] \\ Im[x_i] \end{pmatrix}$ and $V_j = \begin{pmatrix} Re[x_j] \\ Im[x_j] \end{pmatrix}$

From i's property, we know that $||V_i|| \geq ||V_j||, \forall j \in [1,n]$. Then, we have $V_i.V_i \geq V_i.V_j, \forall j \in [1,n]$, ie $Re[x_i]^2 + Im[x_i]^2 \geq Re[x_i]Re[x_j] + Im[x_i]Im[x_j], \forall j \in [1,n]$. Thus, equation (3.8) is a sum of positive terms, and we conclude that $Re[\lambda] \geq e_i > 0$.

All the eigenvalues of B_n have a strictly positive real part, therefore all the eigenvalues of A_n admit a strictly negative real part. System (3.1) has thus a unique and stable solution.

3.5.B Resident-Mutant system

From equation (3.2) and system (3.1) with two populations x_r and x_s, we deduce the following resident-mutant system:

$$\left\{ \begin{array}{lcl} \frac{dq_r}{dt} & = & q_r(\sigma_q \frac{D_rE_r(E_s + C_{r,s}(q_rD_r + q_sD_s))}{(q_rD_r + q_sD_s)(E_rE_s + q_rC_{r,s}D_rE_r + q_sC_{s,r}D_sE_s)} - \gamma) \\ \\ \frac{dq_s}{dt} & = & q_s(\sigma_q \frac{D_sE_s(E_r + C_{s,r}(q_sD_s + q_rD_r))}{(q_sD_s + q_rD_r)(E_sE_r + q_sC_{s,r}D_sE_s + q_rC_{r,s}D_rE_r)} - \gamma) \end{array} \right. \tag{3.9}$$

System (3.9) can be analyzed as a classical population dynamics system. We differentiate two cases:

In the "first come, first served" community ($C_{r,s} = C_{s,r} = 0$), system (3.9) admits two rest points: $\{(q_r^*, 0), (0, q_r^*)\}$. If $D_r > D_s$, $(q_r^*, 0)$ is a stable node, and $(0, q_r^*)$ a saddle point (and inversely if $D_s > D_r$). In this community, system (3.9) converges toward the exclusion of one of the two species (the one with the smallest discovering rate).

In the competitive community ($C_{r,s} = 1 - C_{s,r} \in]0,1[$), system (3.9) admits three rest points: $\{(q_r^*, 0), (0, q_r^*), (q_{rc}^*, q_{sc}^*)\}$, with $q_{rc} = 1 - q_{sc}^* = \frac{\sigma_q D_s(C_{s,r}D_sE_s - C_{r,s}D_rE_r) + \gamma E_rE_s(D_s - D_r)}{\gamma(D_r - D_s)(C_{r,s}D_rE_r - C_{s,r}D_sE_s)}$. Three cases might occur: If $\sigma_q D_r(C_{r,s}D_rE_r - C_{s,r}D_sE_s) + \gamma E_rE_s(D_r - D_s) > 0$ (condition *i*), then rest point $(q_r^*, 0)$ is a stable node, $(0, q_r^*)$ a saddle point and $(q_{rc}^*, q_{sc}^*) \notin \mathbb{R}_+^2$. If $\sigma_q D_s(C_{s,r}D_sE_s - C_{r,s}D_rE_r) + \gamma E_rE_s(D_s - D_r) > 0$ (condition *ii*), then rest point $(0, q_r^*)$ is a stable node, $(q_r^*, 0)$ a saddle point and $(q_{rc}^*, q_{sc}^*) \notin \mathbb{R}_+^2$. Note that conditions *i* and *ii* cannot be both true. Nevertheless, they can be both wrong. In this case, both rest point $(q_r^*, 0)$ and $(0, q_r^*)$ would be saddle points, and $(q_{rc}^*, q_{sc}^*) \in \mathbb{R}_+^2$ would be a stable node. In this kind of community, system (3.9) converges toward either the exclusion of one of the two species, or the coexistence of both species (if neither conditions *i* and *ii* are fulfilled).

3.5.C Strategy classification

To simplify the final expressions, we use the fact that $C_{i,j}$ is a probability distribution, which means that $C_{i,j} + C_{j,i} = 1$. This equality provides some useful simplifications when derived.

From the expression of the invasion fitness $\mathcal{F}_r(s) = \gamma(1 - \frac{D_sE_s(\sigma_q C_{s,r}D_r + \gamma E_r)}{D_rE_r(\sigma_q C_{r,s}D_r + \gamma E_s)})$, we establish the conditions a strategy $x \in [0,1]$ has to fulfill to be a :

Singular Strategy (SS):

$$\frac{\partial \mathcal{F}_r(s)}{\partial s}\Big|_{s=r=x} = 0$$

$$\frac{\gamma E_x(-4\sigma_q D_x^2 C_{x,x}^{(0,1)} + (\sigma_q D_x + 2\gamma E_x)D_x') + \gamma\sigma_q D_x^2 E_x'}{D_xE_x(\sigma_q D_x + 2\gamma E_x)} = 0$$

If a strategy x is a singular strategy, it will be called respectively ESS and CSS if it complies the following properties:

Evolutionary Stable Strategy (ESS):

$$\frac{\partial^2 \mathcal{F}_r(s)}{\partial s^2}\Big|_{s=r=x} < 0$$

$$\frac{\gamma(-2\gamma E_x^3 {D_x'}^2 + \sigma_q D_x^2 {E_x}^2 D_x'' + D_x E_x^2(-\sigma_q {D_x'}^2 + 2\gamma D_x' E_x' + 2\gamma E_x D_x'') - \sigma_q D_x^3({E_x'}^2 + E_x(4E_x C_{x,x}^{(0,2)} - E_x'')))}{D_x^2 E_x^2(\sigma_q D_x + 2\gamma E_x)} < 0$$

Convergence Stable Strategy (CSS):

$$\frac{\partial^2 \mathcal{F}_r(s)}{\partial s^2}\Big|_{s=r=x} \quad > \quad -\frac{\partial^2 \mathcal{F}_r(s)}{\partial s\ \partial r}\Big|_{s=r=x}$$

$$\frac{\gamma(-2\gamma E_x^3 D_x'^2+\sigma_q D_x^2 E_x^2 D_x''+D_x E_x^2(-\sigma_q D_x'^2+2\gamma D_x' E_x'+2\gamma E_x D_x'')-\sigma_q D_x^3(E_x'^2+E_x(4E_x C_{x,x}^{(0,2)}-E_x'')))}{D_x^2 E_x^2(\sigma_q D_x+2\gamma E_x)} \quad > \quad \frac{2\gamma^2 E_x D_x'^2}{D_x^2(\sigma_q D_x+2\gamma E_x)}$$

3.5.D Evolutionary Isoclines

To understand how evolution proceeds once the community becomes dimorphic, we consider a resident community composed of two populations with strategies x_{r_1} and x_{r_2}, and respective abundance $q(r_1)$ and $q(r_2)$. We consider only the coexistence area, then both population abundances reach their respective equilibrium according to the composition of the community. We focus on the introduction of a new rare mutant. Its Invasion fitness in the dimorphic community will be defined as its growth rate when scarce. The pairs (r_1, r_2) where its fitness present an extrema are called evolutionary isoclines (Geritz et al., 1999). If this extrema is a maximum (resp. minimum), the isocline is stable (resp. unstable). The isoclines are the projection in the map (r_1, r_2) of the evolution of the mutant (see Fig. 3.7). The study of these isoclines allows the determination of the direction of evolution.

In our model, the evolutionary isoclines do not cross. We cannot predict a priori the formation of a stable coalition (characterised by the intersection of two stable isoclines). However, after selection has turned disruptive, the new-formed dimorphic population is directed toward the stable isocline (fitness maxima), and tends to move away from the unstable isocline (fitness minima) (Geritz et al., 1999). We consider the map (r_1, r_2), and zoom on one part of the area of coexistence (Fig. 3.7), the other is strictly symmetric by inverting x_{r_1} and x_{r_2}. The isocline standing on the right in Fig. 3.7 1-2 is always unstable. It starts from the point of the boundary of the coexistence area horizontally on the right of the branching point (standing on the diagonal of the map (r_1, r_2)). If the monomorphic dynamics have a repellor point, this isocline will join the point of the boundary of the coexistence area horizontally on the right of the repellor point. If the monomorphic dynamics have no repellor point, this isocline goes down until $x_{r_1} = 0$. The stability of the isocline standing on the left in Fig. 3.7 1-2 depends on the strength of competition. When competition is weak, this isocline is stable (Fig 3.7 1): it starts from the point where the boundary of the coexistence area (locally convex) has an horizontal tangent, and goes down until $x_{r_1} = 0$. When competition is stronger, this isocline starts as stable (as in the weak competition case), but quickly lose its stability (Fig 3.7 2).

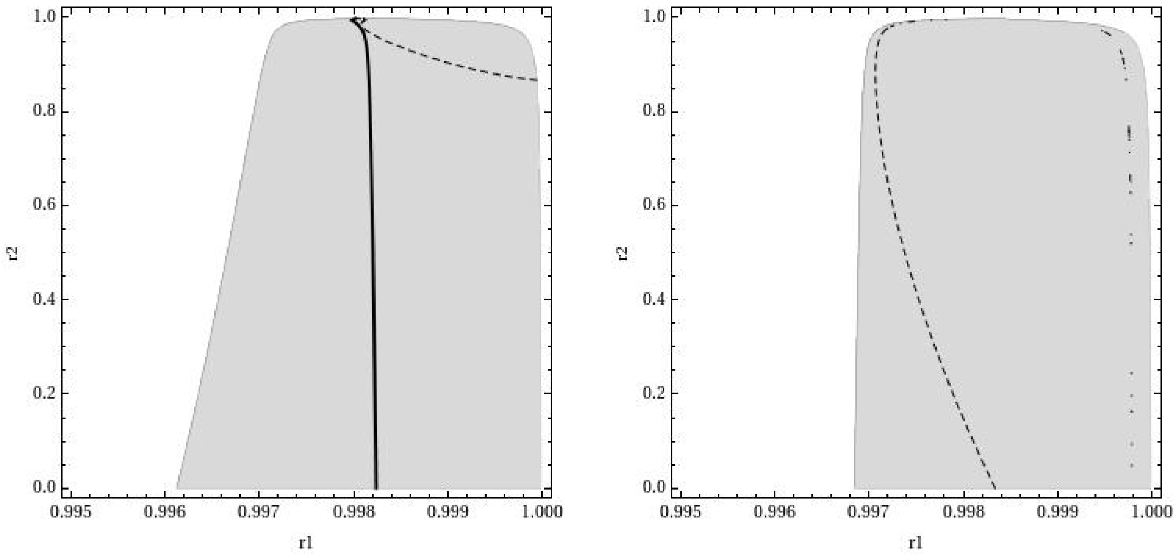


Figure 3.7 — Area of coexistence with the evolutionary isoclines. Thick lines correspond to stable isoclines (fitness maxima), whereas thin dashed lines are the unstable isoclines (fitness minima). 1, food items density $\rho = 0.5$ and asymmetric competition $\phi = 0.01$. 2, food items density $\rho = 0.4$, and asymmetric competition $\phi = 0.1$. Other parameters have been set to $w = 1000, \sigma_q = 0.1, \gamma = 0.001, v = 1, l = 1$.

Two cases might be foreseen. If the asymmetry of competition is weak, evolution might lead the dimorphic population through the (r_1, r_2) map, following the stable isocline trait values (fitness maxima) until reaching the boundary $x_{r_1} = 0$. This state is not a singular coalition, but represents a dimorphic community where no mutant can invade. This scenario occurs in the simulation of the Fig. 3.5 A. If the asymmetry of competition is strong, the outcomes are more aleatory. If the genetic variance is very small (i.e. mutant strategies are very close to the residents), the pair of strategies stay on the stable part of the isocline, and the final outcome of evolution would be a dimorphic community with very similar strategies. If the genetic variance is somewhat higher, the pair of strategies might “escape” the attraction of the stable part of the isocline, and the final outcome would be a dimorphic community with strategy values in the coexistence area between the two unstable isoclines. Several scenarios are possible, as shown in the simulations of the Fig. 3.5 B and 3.5 C. In both cases, even if there is no equilibrium point of the evolutionary process, the dimorphic population will reach a sort of pseudo-stable coalition.

CHAPTER 4

Adaptive dynamics invades ants

4.1 Introduction

Darwin (1859) referred to eusocial insects as “the most serious special difficulty which [his] theory has encountered". The particular challenge of eusocial insects resides in the definition of fitness (see chapter 1). The concept of fitness is underlain by two essential questions of evolutionary biology: i/ “selection of?”, and ii/ “selection for?” (Sober, 1984). In other terms, i/ which is the unit of selection?, and ii/ which is the currency optimised? In sociobiology, the last decades witnessed a long-standing battle regarding units of selection in the evolution of eusociality (see Nowak et al. (2010) and Nanjundiah (2010) for the most recent developments). Some authors defend the concept of genes as the unit of selection, which implies that each colony’s individual maximises its own inclusive fitness (Foster et al., 2006). Other authors define the whole colony as the unit of selection, implying thereby a definition of fitness at the colonial level (Wheeler, 1911; Oster and Wilson, 1978; Wilson and Sober, 1989). Practically, most sociobiologists agree on the need for a pluralistic rather than typological approach that would bridge selfish genes with self-organisation (Ratnieks and Reeve, 1992; Boomsma and Franks, 2006). Nevertheless, some basic features of physiology of the whole colony seem to support the hypothesis of selection at the colony level (Gillooly et al., 2010). Similarly, regarding synergistic behaviours, it might be more pertinent to consider colonies structured by ergonomic efficiency rather than by relatedness (Oster and Wilson, 1978).

Body size is a major phenotypic trait with an essential role in the coexistence of competitors (Brown J.H. et al., 1993; Basset and Angelis, 2007). If the colony is heuristically considered as a "superorganism", with sexuals as germline and workers as soma (Wheeler, 1911), this crucial role would be attributed to the worker number. Indeed, like in unitary organisms, the life history traits of eusocial insect colonies closely depends on the colony mass (defined as the summed mass of all nestmates Hou et al. (2010)). However, "the whole is more than the sum of its part" (Aristotle, Metaphysics, 1045a10), and insect colonies might display complex self-organised patterns (Detrain and Deneubourg, 2006). Nevertheless, collective behaviours depend on positive feedback mechanisms that rely closely on the number of individuals involved. For instance, regarding collective foraging, theoretical works demonstrate that a minimum number of workers is required for recruitment behaviour to be efficient and optimal (Beekman et al., 2001; Sumpter and Beekman, 2003; Planqué et al., 2010). These predictions are confirmed by the noticeable correlation between mature colony size and the sophistication of recruitment behaviour among ant species (Beckers et al., 1989).

In chapter 3, we proposed a model for the evolution of foraging strategies in ants. However, for simplification sake, we assumed that the number of workers was constant and identical for all colonies, independently of their recruitment strategy. Taking into account the importance of colony size (or number of workers), this assumption should be relaxed. This chapter presents a general model of colony fitness that would integrate a fluctuating number of workers. Oster and Wilson (1978) proposed a global framework of colony structure (see Fig. 1.1 in chapter 1), and divide colony life cycle into an ergonomic phase (production of workers), and a reproductive phase (production of sexuals). During the ergonomic phase, the colony produces workers until reaching a certain number. Then, during the reproductive phase, energy is canalised to the production of sexuals. Colony fitness entirely depends on this offspring production and success.

This chapter proposes an implementation of the adaptive dynamics framework for annual eusocial insects. The basic idea stems from the Macevicz and Oster's model 1976: the whole colony is divided into two subunits, reproductives and workers. A major assumption resides in the difference of timescales between worker population growth and colony population growth: worker production is considered to be much faster than colony reproduction. The use of the Implicit Function Theorem allows to correct the fitness gradient of the whole colony according to worker fluctuation. A classification of the singular strategies can thereby be established. This adaptive model is applied to the study of the evolutionary dynamics of recruitment in ants. Simplified fitness functions that account for the Dominance-Discovery trade-off are suggested and analysed in three different cases: i/ a constant number of workers, ii/ a fluctuating number of workers with constant worker-density dependence effect, and iii/ a fluctuating number of workers with strategy-dependent worker-density dependence effect. Evolutionary outcomes are predicted in the different situations, and the emergence and subsistence of diversity of foraging strategies in ant communities is discussed.

4.2 General framework

We propose an adaptive framework of the phenotypical evolution of annual eusocial insects. This framework is limited to clonal reproduction. Phenotypical variability derives from mutations. Mutations are assumed to be so rare as to let the community stabilise at the ecological timescale before the apparition of a new mutant.

4.2.1 The Resident community model

We consider a community composed of a single monomorphic population characterised by a continuous adaptative trait x. Each whole colony of eusocial insects represents an individual. The abundance of the population (ie the number of colonies) is denoted q. The size of individuals (ie the number of workers whithin colonies) is designated as w. The demography of populations q depends on the interactions of single individuals with their surrounding environment. As the interacting units are the workers, the growth rate explicitly depends on the number of workers. Let the function $\mathcal{F}(q, w, x)$ be the population growth rate. The colony population dynamics fluctuate at an annual timescale (t), whereas the inner growth of individuals, ie the worker population demography w, is regulated at a faster timescale (τ). Let the function $\mathcal{G}(q, w, x)$ be the worker production rate.

The dynamics of the community is described by the system (R):

$$(R)\left\{\begin{array}{lcl} \frac{dq}{dt} & = & q\mathcal{F}(q, w, x) \\ \frac{dw}{d\tau} & = & \mathcal{G}(q, w, x) \end{array}\right.$$

As the colony dynamics occur at a far slower timescale than the worker production, we can define a small positive parameter ϵ ($\epsilon \to 0$) such as $dt = \epsilon d\tau$. If we focus on the fast dynamics, system (R) can be rescaled as follows:

$$(R.s)\left\{\begin{array}{lcl} \frac{dq}{d\tau} & = & \epsilon q\mathcal{F}(q, w, x) \\ \frac{dw}{d\tau} & = & \mathcal{G}(q, w, x) \end{array}\right.$$

By setting $\epsilon = 0$, we obtain $\frac{dq}{d\tau} = 0$. Practically, this means that during worker production, the number of colonies can be regarded as a constant. We assume that the worker population dynamics admit a stable and strictly positive equilibrium $\mathcal{W}^*(q, x)$. We assume the worker population dynamics to be independent of the risk of accidental extinction. Indeed, if we modelled the worker population development as birth and death processes, the extinction state 0 would not be an absorbing state. Even if there were no more workers, the queen could still lay eggs and give birth to new workers. Therefore, workers are produced until a stable equilibrium $\mathcal{W}^*(q,x)$ is reached.

Focusing on the slow dynamics, the growth rate of colony population can be established with a unique function $\mathcal{F}(q,\mathcal{W}^*(q,x),x)$. We assume that the population dynamics has a stable and strictly positive equilibrium $q^*(x)$. In a monomorphic community with trait x, the population abundance is assumed to be constant at its equilibrium $q^*(x)$ with a number of workers $w^*(x) = \mathcal{W}^*(q^*(x),x))$.

4.2.2 The Resident-Mutant community model

We now consider a community composed of a resident monomorphic population characterized by a continuous adaptative trait x, and a mutant population, with trait x'. The respective abundance of residents and mutants is q and q', and the size of individuals (i.e. the number of workers in each kind of colony) is respectively w and w'. The community demography is described by the following system:

$$(RM)\left\{\begin{array}{lcl} \frac{dq}{dt} & = & q\mathcal{F}(q,w,x,q',w',x') \\ \frac{dq'}{dt} & = & q'\mathcal{F}(q',w',x',q,w,x) \\ \frac{dw}{d\tau} & = & \mathcal{G}(q,w,x,q',w',x') \\ \frac{dw'}{d\tau} & = & \mathcal{G}(q',w',x',q,w,x) \end{array}\right.$$

The colony population dynamics occur at a far slower timescale. Similarly to the monomorphic case (Resident model R), both q and q' can be regarded as constant for the fast system dynamics W:

$$(W)\left\{\begin{array}{lcl} \frac{dw}{d\tau} & = & \mathcal{G}(q,w,x,q',w',x') \\ \frac{dw'}{d\tau} & = & \mathcal{G}(q',w',x',q,w,x) \end{array}\right.$$

We assume that worker system (W) admits a stable and positive equilibrium. Since the two equations are strictly symmetric, this equilibrium can be noted $(\mathcal{W}(q,x,q',x'),\mathcal{W}(q',x',x,q))$. Before any change occurs in the colony dynamics, the worker system has evolved and reached its stable equilibrium.

At the slow dynamics level, system (RM) is thus equivalent to:

$$(RM.s)\left\{\begin{array}{lcl} \frac{dq}{dt} & = & q\mathcal{F}(q,\mathcal{W}(q,x,q',x'),x,q',\mathcal{W}(q',x',q,x),x') \\ \frac{dq'}{dt} & = & q'\mathcal{F}(q',\mathcal{W}(q',x',q,x),x',q,\mathcal{W}(q,x,q',x'),x) \end{array}\right.$$

4.2.3 The evolutionary model

In the absence of mutants, the Resident-Mutant system degenerates into the Resident-model. Particularly, $\mathcal{W}(q,x,0,x') = \mathcal{W}^*(q,x) = w^*(x)$. Indeed, if absent, mutants do not have any impact neither on the abundance of the resident population, nor on the abiotic environment. Independently of the trait value or the size of the colonies, neither $\mathcal{F}$ nor $\mathcal{G}$ would be affected. Thus, the system (RM) is equivalent to the resident system (R) previously established.

We assume that before the emergence of any mutant population, the resident population is constant at its equilibrium $(q^*(x), w^*(x))$. When a mutant with trait x' slightly different from the resident trait x enters the community, it might either disappear or invade. The fate of mutants is ruled by the *invasion fitness* $\mathcal{S}_x(x')$ (see chapter 2) that represents the per capita growth rate of very scarce mutant population in a community composed exclusively of residents:

$$\mathcal{S}_x(x') = \mathcal{F}(0, \mathcal{W}(x', 0, x, q^*(x)), x', q^*(x), w^*(x), x)$$

$\mathcal{W}(x', 0, x, q^*(x))$ represents the stable equilibrium reached by worker population in the colonies of the scarce mutant population. The Implicit Function Theorem allows to link the partial derivative of the worker equilibrium $(\mathcal{W}(x, q, x', q'), \mathcal{W}(x', q', x, q))$ with the shape of $\mathcal{G}$ (Appendix 4.5.A). All singularity, stability and convergence conditions might thus be determined by the interplay between $\mathcal{F}$ and $\mathcal{G}$. For instance, equation 4.1 explicits the condition for a strategy to be a Singular Strategy (SS). For writing simplification, $\frac{\partial f(x,y)}{\partial x}|_{x=y=z}$ is noted $f^{1,0}(z,z)$, and w^* and q^* refer to $w^*(q^*(x), x)$ and $q^*(x)$.

$$\text{x SS} \quad \Longleftrightarrow \quad \mathcal{F}^{0,0,1,0,0,0}(0, w^*, x, q^*, w^*, x) \; + \; \mathcal{F}^{0,1,0,0,0,0}(0, w^*, x, q^*, w^*, x) \times \frac{\mathcal{G}^{0,0,1,0,0,0}(0,w^*,x,q^*,w^*,x)\mathcal{G}^{0,1,0,0,0,0}(q^*,w^*,x,0,w^*,x)-\mathcal{G}^{0,0,0,0,0,1}(q^*,w^*,x,0,w^*,x)\mathcal{G}^{0,0,0,0,1,0}(0,w^*,x,q^*,w^*,x)}{\mathcal{G}^{0,0,0,0,1,0}(0,w^*,x,q^*,w^*,x)\mathcal{G}^{0,0,0,0,1,0}(q^*,w^*,x,0,w^*,x)-\mathcal{G}^{0,1,0,0,0,0}(q^*,w^*,x,0,w^*,x)\mathcal{G}^{0,1,0,0,0,0}(0,w^*,x,q^*,w^*,x)} \tag{4.1}$$

Since stability (ESS) and convergence (CSS) conditions consist in extremely long formulae, we do not give the details of such conditions in the general case.

4.3 The evolutionary dynamics of foraging strategies

Let $x \in [0, 1]$ be the foraging strategy of the colony. We consider x to be the underpinning feature of the Dominance-Discovery trade-off. For high x values ($x \to 1$), the colony displays high competitive abilities, but is a poor discoverer. Conversely, for low x values ($x \to 0$), the colony is a weak competitor, but is efficient for resource discovery. For instance, x could represent the percentage of recruits within the colony (cf. 3). For convenience of explanation, x is assumed to be species-specific: colonies that share a same strategy x are conspecific.

The Dominance-Discovery trade-off is expressed by two functions $\rho(x)$ and $\alpha(x - x')$. $\rho(x)$ represents the intrinsic growth rate of a colony with strategy x while $\alpha(x - x')$ describes the effect of competition of a colony with strategy x' on a colony with strategy x. The lower the foraging strategy, the higher the intrinsic growth rate ($\rho'(x) < 0$). On the contrary, the higher the difference between $x - x'$, the lower will be the impact of x'-colonies on x-colonies and the higher will be the impact of x-colonies on x'-colonies.

Deterministic analyses without specifying the functions were performed and illustrated by simple examples. In the examples presented, a decreasing linear function was used for $\rho(x)$:

$$\rho(x) = h(1 - x)$$

For $\alpha(x - x')$, the classical concave-convex function was used (Law et al., 1997; Kisdi, 1999).

$$\alpha(x - x') = (1 - h)(1 - \frac{1}{1 + pe^{-k(x-x')}})$$

This function models the effect of an x'-colony on an x-colony. Parameter h ($\in [0, 1]$) refers to the resource. Resource size and density is assumed to be negatively correlated. Increasing h increases resources density, and discovery function ρ. For high values of h ($h- > 1$), resources are small and competition is weaker. Decreasing h ($h- > 0$) increases the size of resources, and the strength of competition (both intra and inter-specific). Parameters k and p shape the intensity of asymmetric competition. k only operates on inter-specific competition and represents the degree of asymmetry between strategies: the higher, the more important will be a small difference of strategies. On the other hand, p applies to both intra and inter-specific competition and will be referred to as competition strength.

The analyses were performed with Wolfram *Mathematica* 7 software.

4.3.1 Constant number of workers

This section presents the simple case where colony size (i.e. worker number) is constant. The colony growth rate involves the intrinsic growth rate $\rho(x)$, the effect of intraspecific competition $\alpha(0)$ weighted by the number of conspecific colonies q, and the effect of inter-specific competition $\alpha(x - x')$ weighted by the number of colonies of the other species q'.

$$\mathcal{F}(q, x, q', x') = \rho(x) - q\alpha(0) - q'\alpha(x - x') \tag{4.2}$$

Adaptive Dynamics analyses allow the identification and the classification of the singular strategies according to the shape of functions ρ and α (Table 4.1). These properties predict the evolutionary outcomes according to the convexity of fitness functions. When assuming specific functions ρ and α, these outcomes can be represented by bifurcation diagrams.

Bifurcation diagrams are graphical tools representing qualitative changes of the long-term regime of a dynamical system in response to a small parameter perturbation. Such representations allow to predict the evolutionary outcomes according to the variation of parameter values. In our system, the interplay between competition strength p and degree of

Table 4.1 — Strategy properties with constant colony size.

PROPERTIES	MATHEMATICAL CONDITION [1]		
SS	$\rho'(x) - \rho(x)\frac{\alpha'(0)}{\alpha(0)}$	$=$	0
ESS	$\rho''(x) - \rho(x)\frac{\alpha''(0)}{\alpha(0)}$	$<$	0
CSS	$\rho''(x) - \rho(x)\frac{\alpha'(0)^2}{\alpha(0)^2}$	$<$	0

[1] Note that these conditions require $\alpha(0) \neq 0$.

asymmetry k determines the long-term evolution (Fig. 4.2). Three main predictions might be made:

i/ When interspecific competition is negligible compared to intraspecific competition ($k << p$), long term evolution leads to individual foraging strategy. There are actually no SS within the range $[0, 1]$, but the boundary strategy $x = 0$ is convergent.

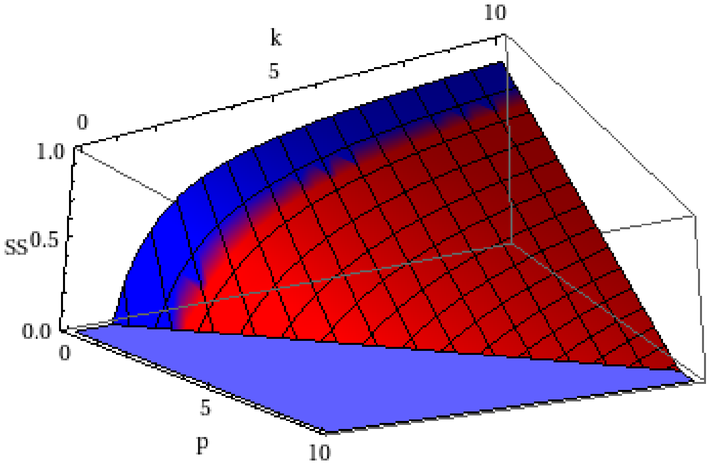
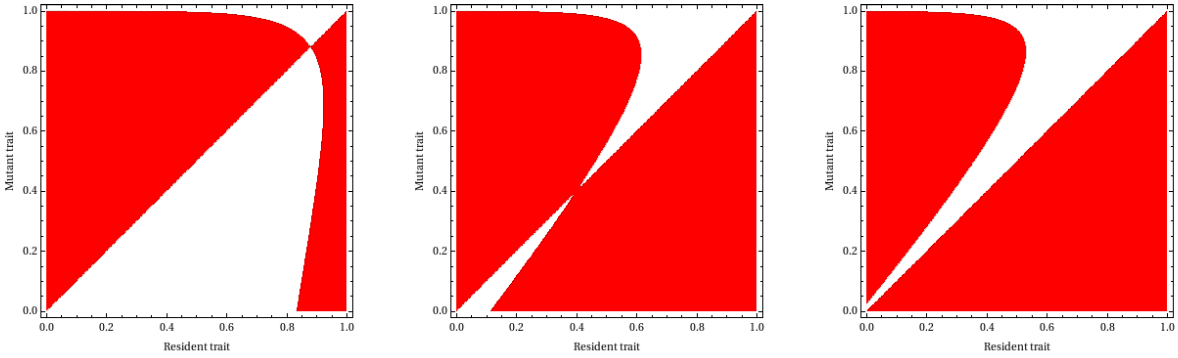


Figure 4.2 — 3D-Bifurcation diagram of the evolutionary outcome regarding the interplay between competition strength and asymmetry degree. The singular strategies are represented according to the combination of values p and k. Singular strategies are coloured according to their evolutionary properties. The blue surface represents evolutionary ending points (both ESS and CSS). Light blue surface represents convergent boundary strategies. The red surface corresponds to evolutionary branching points (CSS, but not ESS). Note that competition strength cannot be null ($p \neq 0$): without competition, the resident population would not be limited $\alpha(0) = 0$ and tend to infinity. The assumption of a stable resident population would be transgressed. These results were not influenced by the environmental parameter h (provided that $h \neq 0$ and $h \neq 1$). In this plot, $h = 0.5$.

ii/ When competition is weak ($p < 1$), a single strategy is selected by long-term evolution. This strategy depends on the degree of asymmetry of competition k: the lower interspecific competition, the lower the foraging strategy. For medium to high values of interspecific competition ($k > 2$), collective foraging is selected ($x > 0.5$).

iii/ When competition strength is higher but remains moderate relative to the degree of asymmetry ($k > p > 1$), the system evolves toward an evolutionary branching point, and directional evolution turns disruptive. The resident community becomes dimorphic.

These predictions are completed by the Pairwise Invasibility Plots (PIP) that represent the sign of the fitness landscape as experienced by a scarce mutant. When this invasion fitness is negative, mutants go extinct. When positive, mutants invade successfully and become the new residents. In the PIPs, the invasion fitness is projected on the two dimensional space generated by the possible resident and mutant trait values. These graphs allow thereby to determine the outcome of successive invasions in a community (Fig. 4.3). The pattern presented in the bifurcation diagram is confirmed. The mental exercise of superposing these plots and their mirror image indicate areas of coexistence between two strategies. The PIP also allow to discriminate the possible coexistence of strategies in a same community.



a/ **weak competition**

b/ **medium competition**

c/ **strong competition**

Figure 4.3 — Pairwise Invasibility Plots. Red areas represent the combination of resident and mutant trait values at which mutant invasion fitness is positive. a/ weak competition ($p = 0.2$): the singular strategy ($x^* \simeq 0.83$) is both convergence and evolutionary stable. A collective recruitment strategy is approached gradually and cannot be invaded locally. b/ medium competition ($p = 5$): the singular strategy ($x^* \simeq 0.4$) is convergent but lacks evolutionary stability. Regardless of the ancestor strategy (i.e. either individual or collective foraging), the branching point is approached gradually and is invaded by any nearby mutants. c/ strong competition ($p = 10$): individual foraging ($x = 0$) is convergent and will be selected under small mutation steps evolutionary processes. However, individual foraging strategy can coexist with all other strategies ($x \in [0.1, 1]$). Other parameter values: $h = 0.5, k = 10$.

The evolutionary scenario once a dimorphic community is reached can be deduced from the analysis of the evolutionary isoclines (see chapter 2). These pair of lines represent sets of singular strategies of the dimorphic community, i.e. the equilibrium strategies where the invasion gradient of scarce mutants vanishes. The growth rate of a colony with strategy x and q conspecifics in a dimorphic community composed of q_1 colonies with strategy x_1 and q_2 colonies with strategy x_2 is defined as follows:

$$\mathcal{F}(q, x, q_1, x_1, q_2, x_2) = \rho(x) - q\alpha(0) - q_1\alpha(x - x_1) - q_2\alpha(x - x_2) \tag{4.3}$$

The convergence and stability of the evolutionary isoclines determine the subsequent evolution of the dimorphic strategy. In the case of medium—weak competition strength (Fig. 4.4), the dimorphic community evolves toward a second branching event. The resident community initially monomorphic will reach higher levels of polymorphism.

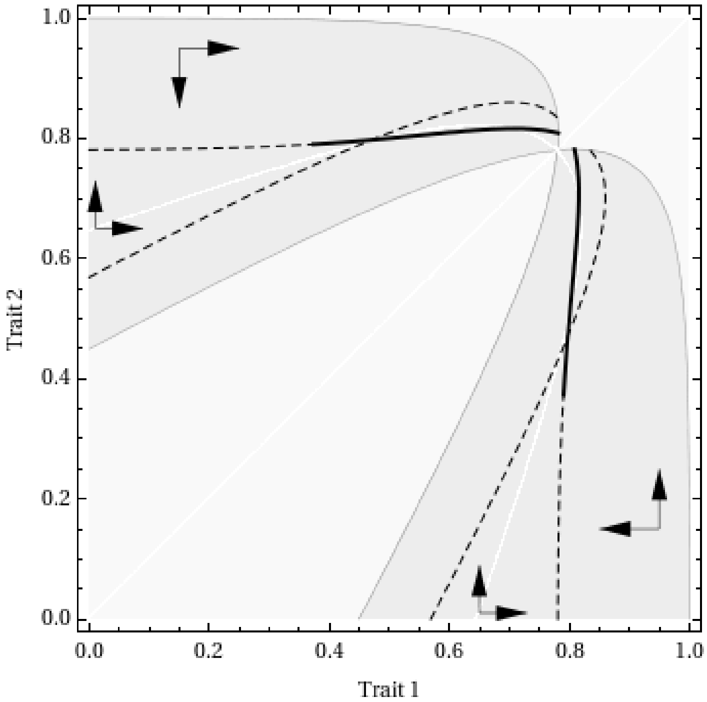
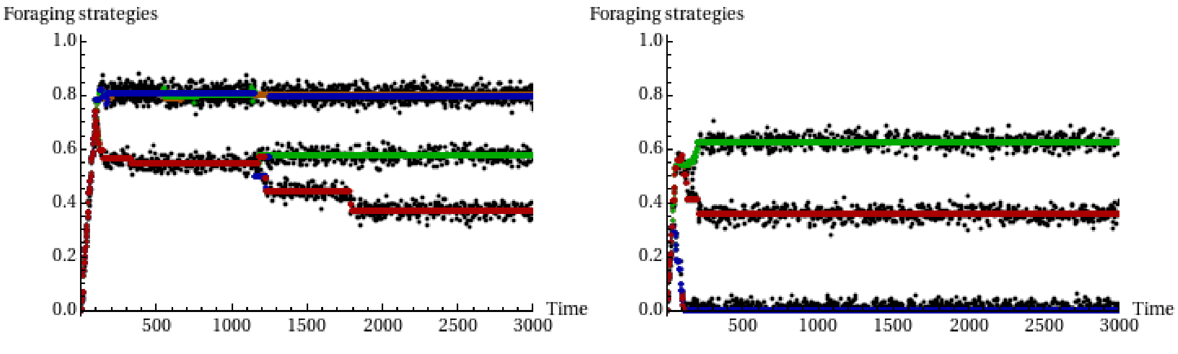


Figure 4.4 — Evolutionary Isoclines under medium competition ($p = 1.2$). Shaded areas represent the region of possible coexistence between traits 1 and 2. The direction of evolution of trait 1 (resp. 2) is shown by horizontal (resp. vertical) arrows. This direction changes when the evolutionary isoclines are crossed. Thick isoclines represent fitness maxima and dashed isoclines are fitness minima. The two isoclines cross at the singular coalition. According to the direction of the arrows, this singular coalition is convergent. Nevertheless, at this coalition, the higher trait value is stable while this lower is unstable. This predicts a second branching event in the dimorphic community. Other parameter values: $h = 0.5$, $k = 10$.

To represent the evolutionary process, stochastic simulations were performed. These simulations consider a community of at most four populations. Each population is represented by a foraging strategy and an abundance of colonies. At each evolutionary time step, a mutation occurs on one of the resident traits. The mutation is a normally distributed random variance with a fixed genetic variance. A scarce mutant population enters the community (mutants abundance is initialised at 1% of the mean colony abundance in the community). The resident-mutant community is let to evolve at the ecological timescale. The populations with trivial abundance are eliminated. The others define the new resident community of the next evolutionary step.

Simulations were performed for different competition intensities (Fig. 4.5). In all cases, evolution started from a monomorphic individually foraging community. For medium values of competition, the initially monomorphic community becomes trimorphic and three populations with different foraging strategies stably coexist. The weaker the strength of competition, the more collective the foraging strategies (higher trait values). With medium—weak competition strength, the three selected strategies are collective whereas in case of medium—strong competition, one of the selected strategy is individual, and the other two are collective.



a/ **medium—weak competition** b/ **medium—strong competition**

Figure 4.5 — Simulated evolutionary trees from individual foraging ancestor strategies. Black points represent unsuccessful mutations. Coloured points represent resident strategies. a/ medium—weak competition ($p = 1.2$). This scenario was predictable from Fig. 4.4. b/ medium—strong competition ($p = 5$). This case correspond to the middle panel of Fig. 4.3. The genetic variance is estimated at 0.02 Evolutionary time is 10,000 times slower than the ecological time. Other parameter values: $h = 0.5$ and $k = 10$.

4.3.2 Fluctuating number of workers with constant worker density dependence

This section relaxes the assumption of constant colony size. Colony population growth rate $\mathcal{F}$ explicitly depends on the within colony worker production rate $\mathcal{G}$. Specifically, functions ρ and α define the per worker intrinsic growth rate and competition effect. The colony growth rate $\mathcal{F}$ involves the intrinsic growth rate $w\rho(x)$, the effect of intraspecific competition $\alpha(0)$ weighted by the number of conspecific workers qw, and the inter-specific competition $\alpha(x-x')$ weighted by the number of workers of the other species $q'w'$. The development of worker population $\mathcal{G}$ also depends on the intrinsic colony growth rate. However, we assume that the production of workers is independent of the interaction with neighbour colonies. Since worker production often declines as the worker population reaches its highest level, worker production is assumed density-dependent (Oster and Wilson, 1978; Hölldobler and Wilson, 1990). Parameter μ ($\mu > 0$) includes the effect of density-dependence on the within colony growth.

$$\begin{cases} \mathcal{F}(q,w,x,q',w',x') = w\rho(x) - qw\alpha(0) - q'w'\alpha(x-x') \\ \mathcal{G}(q,w,x,q',w',x') = w\rho(x)(1-\mu w) \end{cases} \tag{4.4}$$

The general model presented above (see 4.2) enables to identify the singular strategies (SS) and their evolutionary properties according to the shape of both $\mathcal{F}$ and G. The establishment of such properties with the functions specified in system (4.4), allows to classify the SS according to the shape of functions ρ and α (Table 4.6). Provided parameter μ is positive, these conditions are strictly equivalent to those defined for a constant worker population (see 4.3.1). The evolutionary outcomes according to ρ and α convexity is thus analogous to the constant worker case. The example given with specific functions in the bifurcation diagram is still valid in the context of a fluctuating number of workers with constant worker density dependence (Fig. 4.2).

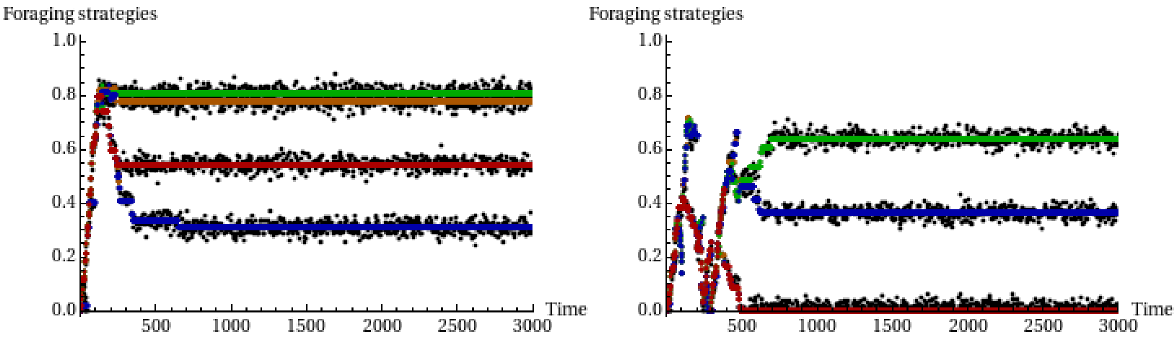
Table 4.6 — Strategy properties with variable colony size depending on fixed worker density-dependence.

PROPERTIES	MATHEMATICAL CONDITION [2]		
SS	$\rho'(x) - \rho(x)\frac{\alpha'(0)}{\alpha(0)}$	$=$	0
ESS	$\rho''(x) - \rho(x)\frac{\alpha''(0)}{\alpha(0)}$	$<$	0
CSS	$\rho''(x) - \rho(x)\frac{\alpha'(0)^2}{\alpha(0)^2}$	$<$	0

[2] Note that these conditions require $\alpha(0) \neq 0$ and $\mu > 0$.

In this case, the interplay between competition strength p and degree of asymmetry k has thus the same influence on the long-term evolution as in the case of constant colony size (4.3.1). To check these predictions, stochastic long-term simulations were performed. As previously, simulations consider a community of maximum four populations, and the ecological outcome of population dynamics determines the evolutionary outcome of strategy evolution. The only difference with the previous system resides in the population dynamics. This ecological time scale dynamics involves a double process: a fast within colony worker production and a slow colony dynamics. In the simulations, colony development is based on the equilibrium number of workers.

Simulations were performed in the same conditions as previously and show the same global patterns (Fig. 4.7). In all cases, a monomorphic community (with individual strategy as initial strategy) becomes polymorphic.



a/ **medium—weak competition** b/ **medium—strong competition**

Figure 4.7 — Simulated evolutionary trees from an individual foraging ancestor strategy. Colony growth explicitly includes worker growth. Black points represent unsuccessful mutations. Coloured points represent resident strategies. a/ medium—weak competition ($p = 1.2$). b/ medium—strong competition ($p = 5$). The genetic variance is estimated at 0.02 Evolutionary time is 10,000 times slower than the ecological time. Other parameter values: $h = 0.5$, $\mu = 0.01$ and $k = 10$.

4.3.3 Fluctuating number of workers with variable worker density dependence

This section relaxes the assumption of constant density-effect. Practically, density-effect μ is considered to be a function of the foraging strategy x. The colony growth rate $\mathcal{F}$ still depends on the intrinsic growth rate $w\rho(x)$, on the overall effect of intraspecific competition $qw\alpha(0)$, and on the overall effect of inter-specific competition $q'w'\alpha(x-x')$. The devolpment of the worker population $\mathcal{G}$ depends on the intrinsic colony growth rate and on function $\mu(x)$ that includes the effect of density-dependence on the within colony growth.

$$\begin{cases} \mathcal{F}(q,w,x,q',w',x') = w\rho(x) - qw\alpha(0) - q'w'\alpha(x-x') \\ \mathcal{G}(q,w,x,q',w',x') = w\rho(x)(1-\mu(x)w) \end{cases} \tag{4.5}$$

Like in the previous section, the general model (see 4.2) was adapted to the specified shape of $\mathcal{F}$ and G defined in system (4.4). Singular strategies are identified and classified according to the shape of functions ρ, α and μ (Table 4.8).

Table 4.8 — Strategy properties with variable colony size depending on variable worker density-dependence.

PROPERTIES	MATHEMATICAL CONDITION [3]		
SS	$-\rho(x)\frac{\mu'(x)}{\mu(x)} + \rho'(x) - \rho(x)\frac{\alpha'(0)}{\alpha(0)}$	$=$	0
ESS	$-2\rho'(x)\frac{\mu'(x)}{\mu(x)} + \rho''(x) - \rho(x)\frac{\alpha''(0)}{\alpha(0)}$	$<$	0
CSS	$-\rho(x)\frac{\mu''(x)}{\mu(x)} + \rho''(x) - \rho(x)\frac{\alpha'(0)^2}{\alpha(0)^2} - 2\rho(x)\frac{\alpha'(0)\mu'(x)}{\alpha(0)\mu(x)}$	$<$	0

[3] Note that these conditions require $\alpha(0) \neq 0$ and assume $\mu(x) > 0$.

In the examples developed, function $\mu(x)$ was assumed to decrease with foraging strategy: the more collective the strategy, the less the worker production was impeded by high worker density. A linear function was used:

$$\mu(x) = \nu(2 - x)$$

Applying the different evolutionary predictions (Table 4.8) to the specified functions, the long-term evolution can be determined according to parameter values (Fig. 4.9). The bifurcation diagram in a variable worker density-dependence context present a general pattern similar to the case of constant colony size. Nevertheless, the three main predictions should be slightly modulated:

i/ When the degree of asymmetry is weak ($k < 5$) and negligible compared to intraspecific competition ($k << p$), the long term evolution selects individual foraging strategies.

ii/ When competition strength is weaker than a critical value, a single strategy is selected. The critical value rises while decreasing interspecific competition value (for $k = 10$, the critical value is $p = 1$; for $k = 4$, the critical value is $p = 3.5$). The value of the selected strategy decreases with the degree of competition asymmetry k: the lower interspecific competition, the less collective the foraging strategy.

iii/ When competition strength is higher than the critical value and interspecific competition is either strong ($k > 5$) or higher than the competition strength ($k > p$), the monomorphic community evolves toward a branching point. Globally, the conditions of parameters allowing such events are wider in this context than in the case of constant colony size.

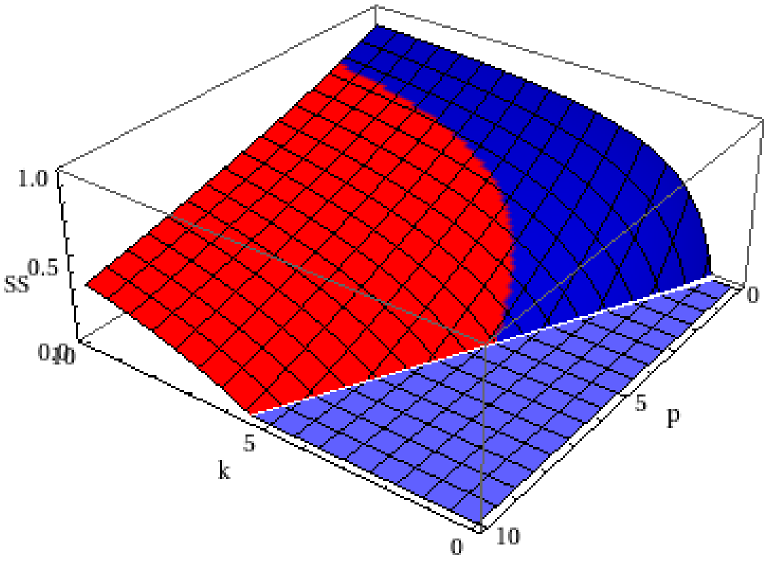
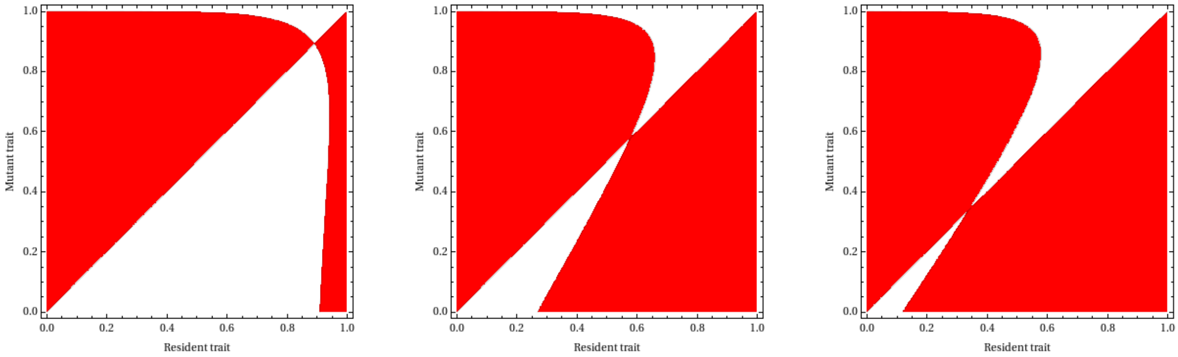


Figure 4.9 — 3D-Bifurcation diagram of the evolutionary outcome of the interplay between competition strength and degree of asymmetry with explicit worker growth. Singular strategies are plotted according to the combination of parameters p and k. Colours represent the nature of the SS: in blue, evolutionary ending points (both ESS and CSS); in light blue, convergent boundary strategies; and in red, branching points (CSS, but not ESS). Limit case $p = 0$ is not to consider since it does not respect the assumption of resident population stability. Other parameter values: $h = 0.5$ and $\nu = 0.01$.



a/ **weak competition** b/ **medium competition** c/ **strong competition**

Figure 4.10 — Pairwise Invasibility Plots. Red areas represent positive invasion fitness. a/ weak competition ($p = 0.2$): directional evolution stop at the singular strategy ($x^* \simeq 0.9$) that is both CSS and ESS. b/ medium competition ($p = 5$): directional selection turns disruptive at the branching point ($x^* \simeq 0.6$). c/ strong competition ($p = 10$): the monomorphic community evolve toward the branching point ($x = 0.35$) and becomes dimorphic. Other parameter values: $h = 0.5$, $k = 10$, and $\nu = 0.01$.

As mentioned above, Pairwise Invasibility Plots present the combination of mutant and resident traits allowing mutant invasion. The invasion fitness considers the growth rate of a scarce mutant population in a resident community at equilibrium (4.2). Mutant colony size is the equilibrium number of workers in a resident community at equilibrium. The PIP presented in Fig. 4.10 allows a direct comparison with the case of constant colony size. In the case of weak competition, the foraging strategy selected by directional evolution is more collective than in the case of constant colony size. Under medium competition, the value of the branching point is also higher: an evolutionary process starting with an individual foraging strategy would first reach a more collective strategy before becoming polymorphic. With strong competition, the nature of the singular strategy is different. In the case of constant colony size, individual foraging strategy was selected. In this case, the resident community first evolves toward a collective strategy and becomes dimorphic by disruptive selection.

To establish the evolutionary isoclines, the dimorphic population should be considered at equilibrium. The first step in the analysis of a community with two strategies x_1 and x_2 is to determine the equilibrium numbers of workers w_1^* and w_2^* and the equilibrium numbers of colonies q_1^* and q_2^*. In a resident community composed in this way, the growth rate of a colony with strategy x, w workers and q conspecifics is:

$$\begin{aligned}
\mathcal{F}(q,w,x,q_1^*,w_1^*,x_1,q_2^*,w_2^*,x_2) &= w\rho(x) - qw\alpha(0) - q_1^*, w_1^*\alpha(x-x_1) - q_2^*, w_2^*\alpha(x-x_2)\\
\mathcal{G}(q,w,x,q_1^*,w_1^*,x_1,q_2^*,w_2^*,x_2) &= (w\rho(x) - qw\alpha(0) - q_1^*, w_1^*\alpha(x-x_1) - q_2^*, w_2^*\alpha(x-x_2))(1-\mu(x)w)
\end{aligned} \tag{4.6}$$

The growth rate of a scarce mutant is obtained with $q = 0$ and by taking w at its equilibrium. This function was used to represent the isoclines in order to establish the evolutionary outcome in the dimorphic community (Fig. 4.11). With medium competition strength, the dimorphic community evolves toward a convergent singular coalition of strategies that is evolutionary unstable, predicting the occurrence of more branching events.

Simulations were performed as in the case of constant density-dependence. The evolution of strategies is driven by interactions at the ecological level that depend on both slow colony dynamics and fast worker dynamics. With medium competition, the initially monomorphic community undergoes several branching events and reaches the highest level of polymorphism allowed by the simulation algorithm (four resident populations) (Fig. 4.12.a). These four resident strategies stably coexist: individual foraging, recruitment with low degree of cooperation, recruitment with medium degree of cooperation, and recruitment with high degree of cooperation.

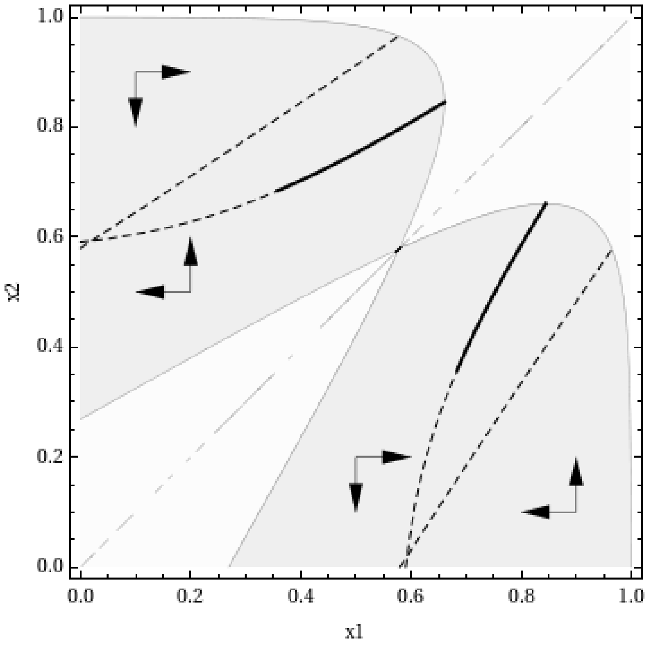
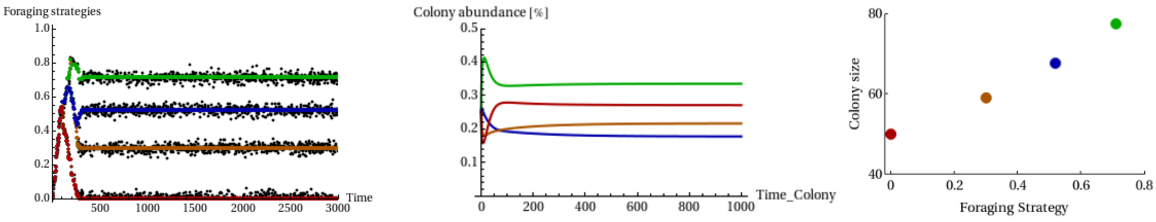


Figure 4.11 — Evolutionary Isoclines under medium competition ($p = 5$). Shaded areas represent the region of possible coexistence between traits 1 and 2. The direction of evolution on trait 1 (resp. 2) is shown by horizontal (resp. vertical) arrows. Thick isoclines represent fitness maxima and dashed isoclines are fitness minima. The singular coalition (point where isoclines cross) is convergent and represent a fitness minima for both trait values predicting further branching events. Other parameter values: $h = 0.5$, $k = 10$, and $\nu = 0.01$.



a/ **evolutionary tree** b/ **colony abundance** c/ **colony size**

Figure 4.12 — Evolutionary outcomes from a monomorphic community with individual foraging strategy. a/ Simulated evolutionary tree. The community reaches high degree of polymorphism. Note that four resident populations is the maximum allowed by the technique used for simulation. b/ Respective equilibrium abundance of the resident populations (corresponding colours) relatively to the total abundance within the community. c/ The respective equilibrium colony size of the resident populations (corresponding colours) is negatively correlated to the foraging strategy: the most collective the foraging strategy, the highest the number of workers within the colony. Other parameters: $h = 0.5$, $k = 10$, and $\nu = 0.01$.

At equilibrium, the respective abundance (i.e. proportional number of colonies) depends on the foraging strategy (Fig. 4.12.b). The most abundant species is the species using recruitment with highest degree of cooperation, the second most abundant is the individually foraging species, the third is the species recruiting with low degree of cooperation and the fourth is the species recruiting with medium degree of cooperation. The colony size at equilibrium is positively correlated with the degree of cooperation (Fig. 4.12.c). The higher the degree of cooperation, the higher the equilibrium colony size.

4.4 Discussion

This chapter presents a theoretical framework for the study of the evolutionary dynamics of life history traits or specific behaviours in annual eusocial insects. An example considering the evolutionary dynamics of foraging strategies in ants is developed. It shows how a simple trade-off between intrinsic growth rate and competitive ability might explain the emergence and maintenance of very different strategies in a same community depending on the interplay between intra and inter specific competition. Besides, a trade-off between colony intrinsic growth rate and colony worker density-dependence explains the difference of colony size according to the foraging strategy.

The central aim of this work was to show how Adaptive Dynamics theory could be applied to annual eusocial insect societies. The classical model of Macevicz and Oster (1976) considers a colony divided into workers and sexuals, and defines fitness as the rate of production of sexuals. Our model is inspired by this work but considers insect societies in a more abstract perspective. The whole colony is defined as an unity per se. This colony is dependent though on its size, i.e. the number of workers. The simplifying assumptions consider that colony development (i.e. worker production) is faster than colony reproduction (i.e. production of new colonies). Colony development and reproduction are defined by a slow-fast system of differential equations that represent the colony population dynamics. Interactions between different colony populations define the community dynamics. This dynamics at the ecological timescale drives the evolutionary process at the evolutionary timescale (Fig. 4.13).

The example presented emphasises the importance of trade-offs between intrinsic growth and competitive abilities in both the emergence and the coexistence of different strategies in a same community. Trade-offs between competitive abilities and other fitness components such as mortality (Adler and Mosquera, 2000), colonisation abilities (Tilman, 1994; Calcagno et al., 2006), or resource exploitation (Amarasekare, 2002; Adler et al., 2007) are often suggested as an explanation for species coexistence. Besides, the emergence of different species (or set

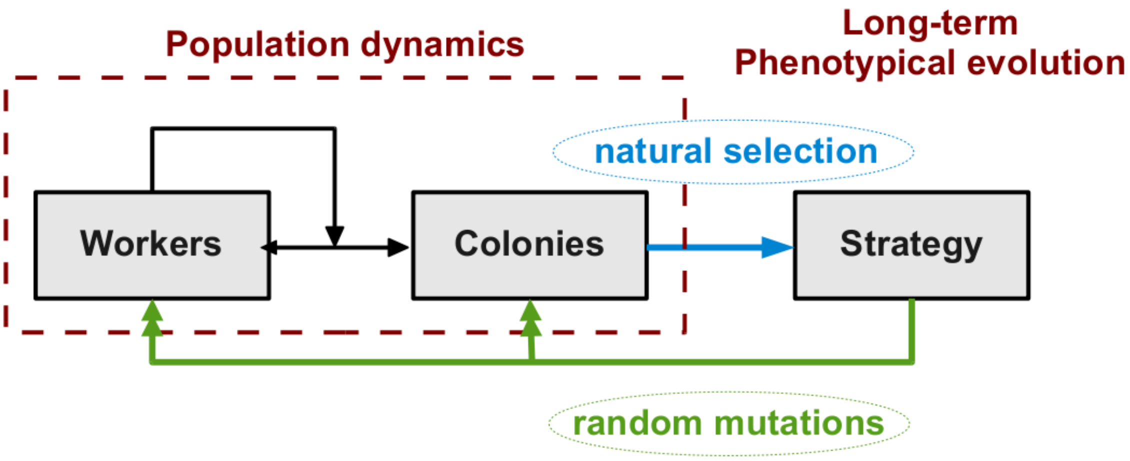


Figure 4.13 — Schematic representation of Adaptive Dynamics applied to annual eusocial insects. The colony population dynamics is defined by both worker production and colony reproduction. Random mutations occur on strategies and mutant colonies enter the community. The interactions of colonies at the ecological timescale drive the evolution of strategies at the evolutionary timescale by natural selection.

of individuals using a given strategy) can be made possible by the degree of competition asymmetry in such trade-off (Law et al., 1997; Kisdi, 1999). In the present work, asymmetric competition underpins both the emergence and coexistence of different foraging strategies. These strategies are involved in a trade-off between intrinsic colony growth and competitive ability on the one hand, and intrinsic colony growth and worker density dependence on the other. A criticism could be raised about the assumption made that worker production is not subject to competition. Other population dynamics systems might be developed to assess the importance of such an assumption on the evolutionary dynamics.

The evolutionary results of this work are somewhat surprising. Since collective foraging species are better competitors, we could have expected that strong competitive pressure would favour the evolutionary stability of collective foraging strategies. In contrast, collective foraging is selected when competition is weak. When the general competition strength (both intra and interspecific) is strong relatively to the interspecific competition, an individual foraging strategy is selected. Otherwise, intermediate competition strength drives the initially monomorphic community to become polymorphic. Regardless of the ancestor strategy, foraging evolves toward a strategy involving an intermediate degree of cooperation. However this strategy is not evolutionary stable, and negative frequency-dependent selection favours the apparition of different strategies that diverge. The stable community composition at the end of the evolutionary process depends on the strength of competition. Generally, the stronger the competition effect, the less collective are the foraging strategies. To sum up, even a simple model might explain the apparition and the coexistence of foraging strategies involving different degrees of collective behaviour as it occurs in ant communities with foraging strategies such as individual foraging, tandem running, group recruitment, and mass recruitment (see chapter 1).

Many studies on the optimality of collective foraging behaviour coincide on the importance of the number of individuals and conclude that collective foraging is optimal for large colonies (Beekman et al., 2001; Sumpter and Beekman, 2003; Planqué et al., 2010). Since the establishment of a positive correlation between colony size and the degree of communication in ant foraging behaviour (Beckers et al., 1989), the trend seems to be a one-way question: Tell me your colony size, I will tell you your optimal foraging strategy. The model with an explicit function for worker growth relaxes the necessity of preliminary assumptions on colony size. Furthermore, colony size might be predicted as an evolutionary outcome. When a trade-off between intrinsic colony growth rate and the effect of density dependence is involved, the predicted colony sizes are positively correlated with the degree of cooperation of the foraging strategies. Nevertheless, the pertinence of such a trade-off in nature could be questioned. Is the degree of cooperation considered in the foraging process linked to the eventual egg-laying limitation of the queen? Are collective foraging species more likely to be polygynic (several queens per colony)? Are the workers of collective foraging species smaller and less costly to produce? Do collective foraging species display more chemical sensitivity and thereby have bigger nests without loosing the colonial cohesion? Anyway, even if the biology is far from being totally understood, this general model can serve as an heuristic basis to reverse the trend: tell me your trade-off, I will tell you both your foraging strategy and your colony size.

4.5 Appendix

4.5.A The Implicit Function Theorem applied to workers production

When considering the Resident-Mutant community dynamics at the slow timescale, two systems should be considered. The first one is the rescaled system ($RM.s$). The second system ($W.s$) deals with worker production functions:

$$(W.s)\left\{\begin{array}{rcl} 0 & = & \mathcal{G}(q,w,x,q',w',x') \\ 0 & = & \mathcal{G}(q',w',x',q,w,x) \end{array}\right.$$

We assume that all the mild conditions on $\mathcal{G}$ partial derivative that are necessary to the application of the Implicit Function Theorem are fulfilled.

Let Q and P be respectively

$$Q = \begin{pmatrix} \frac{\partial \mathcal{G}(q,w,x,q',w',x')}{\partial w} & \frac{\partial \mathcal{G}(q,w,x,q',w',x')}{\partial w'} \\ \frac{\partial \mathcal{G}(q',w',x',q,w,x)}{\partial w} & \frac{\partial \mathcal{G}(q',w',x',q,w,x)}{\partial w'} \end{pmatrix}$$

and

$$P = \begin{pmatrix} \frac{\partial \mathcal{G}(q,w,x,q',w',x')}{\partial q} & \frac{\partial \mathcal{G}(q,w,x,q',w',x')}{\partial x} & \frac{\partial \mathcal{G}(q,w,x,q',w',x')}{\partial q'} & \frac{\partial \mathcal{G}(q,w,x,q',w',x')}{\partial x'} \\ \frac{\partial \mathcal{G}(q',w',x',q,w,x)}{\partial q} & \frac{\partial \mathcal{G}(q',w',x',q,w,x)}{\partial x} & \frac{\partial \mathcal{G}(q',w',x',q,w,x)}{\partial q'} & \frac{\partial \mathcal{G}(q',w',x',q,w,x)}{\partial x'} \end{pmatrix}$$

Provided that $det(Q) \neq 0$, the Implicit Function Theorem gives us the following conclusions:

- $(W.s) \iff \exists\phi$ such as $(w, w') = \phi(q, x, q', x')$
- ϕ's Jacobian matrix $J = -Q^{-1}P$

Since $(w, w') = (\mathcal{W}(x, q, x', q'), \mathcal{W}(x', q', x, q))$, we can identify the partial derivatives of $\mathcal{W}$ according to (q, x, q', x') with the values of J (ϕ's Jacobian matrix).

$$J = \begin{pmatrix} \frac{\partial \mathcal{W}(x,q,x',q')}{\partial q} & \frac{\partial \mathcal{W}(x,q,x',q')}{\partial x} & \frac{\partial \mathcal{W}(x,q,x',q')}{\partial q'} & \frac{\partial \mathcal{W}(x,q,x',q')}{\partial x'} \\ \frac{\partial \mathcal{W}(x',q',x,q)}{\partial q} & \frac{\partial \mathcal{W}(x',q',x,q)}{\partial x} & \frac{\partial \mathcal{W}(x',q',x,q)}{\partial q'} & \frac{\partial \mathcal{W}(x',q',x,q)}{\partial x'} \end{pmatrix}$$

Equality $J = -Q^{-1}P$ gives us the expression of $\mathcal{W}$'s partial derivatives according to the shape of $\mathcal{G}$.

CHAPTER 5

Do we need accurate models?

5.1 What did we learn from the Dominance-Discovery trade-off?

In this part, we proposed two different models of the evolutionary dynamics of foraging strategies in ants. In both cases, the foraging strategy was a continuous trait representing the degree of cooperation while foraging. This strategy underpinned the Dominance-Discovery trade-off: the higher the degree of cooperation, the higher the competitive ability, but the slower the discovery. Both approaches demonstrated that this trade-off could account for the emergence and the persistence of different foraging strategies in a sympatric ant community.

The essential component to explain foraging strategy polymorphism was competition. In both models, stronger competitive asymmetry extends the parameters range allowing the community to reach higher polymorphic levels. The second model specifies that the evolutionary dynamics might be driven by the interplay between intra and inter competition. Practically, inter-specific competition has to be stronger enough relatively to intra-specific competition to explain strategy diversity. These results confirm the essential part played by the competitive trade-off.

In both models, the evolutionary dynamics was assessed through an adaptive dynamics approach. This theoretical framework is very powerful to predict deterministically stochastic evolutionary outcomes. However, it might be considered as restrictive since mutations are assumed to be small, rare, and population polymorphism is reduced. Nevertheless, even when relaxing these assumptions using individual based simulation models, a simple trade-off explains foraging strategy diversification (Fig. 5.1).

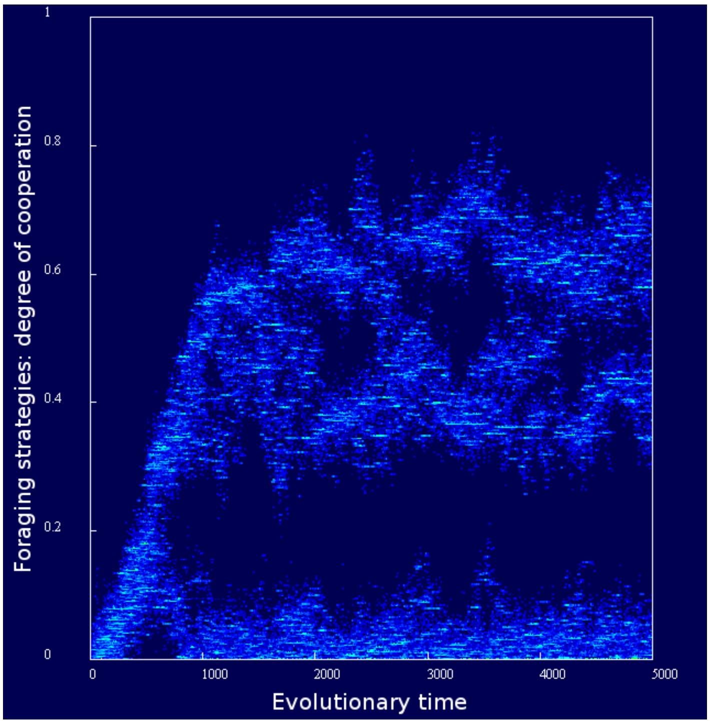


Figure 5.1 — Simulated evolutionary tree with ZEN, the eco-evolutionary software (Legendre, 2002). ZEN is a generic individual based program that simulates the evolution of phenotypes under mutation-selection processes. The dynamics of finite populations is described by stochastic equations in discrete time. The model of chapter 4 (with constant colony size) was translated into a discrete model with integer colony population sizes. $n(t+1) = \mathcal{P}oisson(n(t), f)$ with $f = exp(\mathcal{F})$ (see eq. 4.2 for $\mathcal{F}$ definition). In this simulation, mutation rate was 0.02, and standard deviation in the distribution of mutations was 0.02. Other parameter values: $p = 5, h = 0.5, k = 10$.

The first model (chapter 3) was more accurate and explicited the importance of the environment regarding both the size and the distribution of resources. Earlier studies suggest that patch size is more important than patch density (Johnson et al., 1987; Jaffe and Deneubourg, 1992). However, since the model assumed a negative correlation between size and density, this model cannot make the difference between the two characteristics. The evolutionary model though predicts that resources must be small enough or dense enough for diversity to emerge.

The second model (chapter 4) presented a model dividing the colony growth into an inner development dynamics (worker production) and a reproductive dynamics (colony reproduction). Assuming that the strategy does not have the same impact on both dynamics could explain at the evolutionary level, the emergence of species with different foraging strategies and different colony size. Besides, the degree of polymorphism the community reached was higher when workers growth rate explicitly differ from colonies intrinsic growth rate. The intrinsic allocation conflict in the colony could thus be a mechanism to explain species diversity in ant communities.

5.2 How could we have learnt more?

The model presented in chapter 3 intended to account for realistic foraging processes. Taking into account all the complexity of both colony foraging and colony interaction at food source is though impossible in a simple determinist model, and reality has been sacrificed. Nevertheless, being aware of these limits is essential to weight the predicted results and develop further improvements.

The most important criticism regards the size of food items. In the patch dynamics presented (System 3.1), the size of food items is fixed. A food item usurped from a weaker competitor has exactly the same size as a food item discovered for the first time. However, once discovered, a food item is harvested and its size should progressively decrease. Not taking this size reduction into account gives an indisputable advantage to collective foragers since they do not loose anything because of late discovery. Different solutions would take these features into account. The first possibility would be to correct $C_{i,j}R_j$, the number of food items usurped by colony i to colony j, by E_j, the exploitation ability of species j. For example, a decreasing function could be used such as $\frac{C_{i,j}R_j}{1+E_j}$. The second solution would be to structure patch population by size. This solution is more elegant but far more difficult to model.

The first limit gives an advantage to collective foragers, but the second criticism balances the score by favouring individual foragers. In the model, scouts were assumed to harvest a patch once discovered. The literature about the scout-recruit concept is not very clear about this assumption and the division of labour between searching and exploiting might not be so clear (Biesmeijer and de Vries, 2001). This could also depend on the studied species. An alternative to the scout-recruit dilemma could be to focus on the information spread with a dichotomy between informed or uninformed ants (Adler and Gordon, 1992). Nevertheless, in our model, if scouts were not able to harvest the patch, this would also deprive individual foragers of memory since they would not be able to come back to a discovered resource. This would be clearly wrong (Wehner and Räber, 1979). Scouts were thus allowed to harvest discovered food items. However, the model does not differentiate harvesting scouts from searching scouts and in the function used, scouts are both searching and harvesting. The number of searching scouts on a colony of species i should not be $w(1-x_i)$ but rather $w(1-x_i)-R_i$.

In all the foraging processes, a gross approximation is made on the distance between the nest and the food source. However, if distance probably decreases with food item density, distance should increase with the number of discovered items. Moreover, nests distribution is probably also important in competitive interactions. A spatial structure of both resources and nests would be required to study the importance of space in the importance of exploitation and dominance of dispersed food sources (Tilman, 1994; Amarasekare, 2003).

The absence of competition from other agents than ants could also be criticised. Competition with other agents includes exploitative or interference competition with other animals, but also the self perisher of resources. Indeed, in our model, nothing limits resource development but ants. Thus, without ants the number of food items would tend to infinity. Infinite availability of resources is never realistic. This problem can though be easily fixed by adding a disappearing rate of resource, such as the parameter $-b$ in Adler et al.'s model (2007).

Conversely, the model presented in chapter 4 did not aim to be realistic. It was based on generic trade-off functions and examples were provided with simple functions such as the flexible convex-concave function used in the competitive abilities. Since no biological studies support the use of such functions, the predictions provided by the example are nothing but heuristic considerations. More accurate measures of competitive interactions would be needed to connect our models to community ecology (Abrams, 2001b). Without such data, a more general discussion either based on the geometry (de Mazancourt and Dieckmann, 2004) or on a critical function analysis (Geritz et al., 2007) could have been pertinent.

The last important limit to be aware of comes from the very definition of foraging strategy. In both models, foraging strategies are specific and constant for a given individual. The assumption was supported by theoretical results demonstrating that only one recruitment method is likely to be used consistently (Planqué et al., 2010). Nevertheless, real ant colony might switch their foraging strategy according to the maturity of colony (Mailleux et al., 2003) or to the kind of resources (Bernstein, 1975; Cerdá et al., 2009) or to the presence of competitors (Putyatina, 2007). Would this foraging strategy plasticity change the evolutionary outcomes predicted?

5.3 To learn more or to learn better?

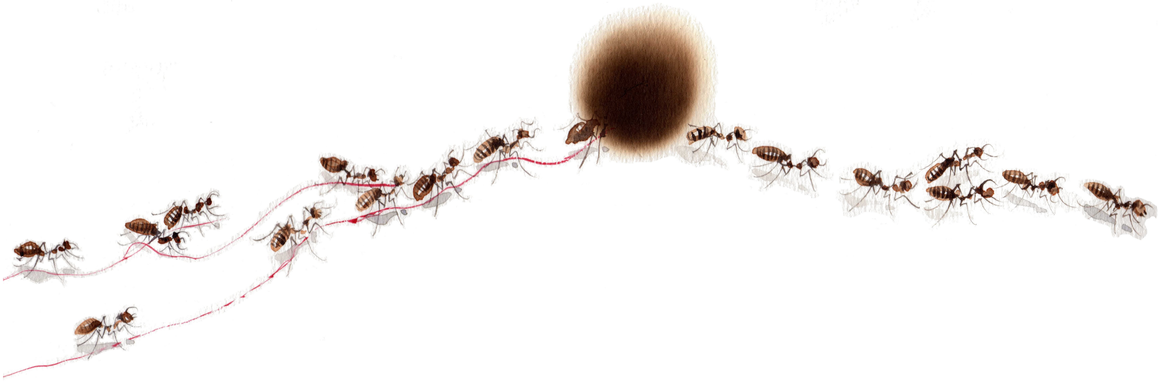
To conclude about this theoretical exploration of the Dominance-Discovery trade-off, I propose a brief reflexion about the optimal degree of complexity theoretical models should achieve. Models are submitted to a severe trade-off between accuracy and simplicity and theoreticians might often hesitate to optimise their model accuracy. Do we actually need accurate models?

This question might sound absurd: we might think that the more accurate the models are, the best they describe a biological situation. However, improving model accuracy often rhymes with increasing the number of parameters and giving up linear and smooth functions, which implies implicitly, apart from terrific headaches, more flexibility in the predicted outcomes. Very accurate models with a huge amount of interacting variables are computable. Outcomes are predicted according to the interplay of parameters. Nevertheless, when no data are available on the focused situation, there might always exist a set of parameters allowing the expected outcome. In other terms, too accurate models cannot fail.

In the hypothetico-deductive approach, the basic idea is to emit hypotheses. Theoretical models help defining an hypothesis. They have to be simple enough for their predictions to be tested. When models fail, the assumptions are reevaluated and the heuristic dynamics starts. That is what explains Kacelnik's “perverse delight in the failure of optimality models" (1993). The true interest of theoretical models resides in their limits. They do not aim to give any definitive answers, but to challenge biologists.

Part II

The Dominance-Thermal Tolerance Trade-off



Introduction

In this part, we focus on the Dominance-Thermal tolerance trade-off in Mediterranean ant communities. As specified in the general introduction (see 1.2.2), behaviourally dominant species tend to be less tolerant to high temperatures than subordinates. Besides, dominants generally forage at temperatures far lower from their physiological limit than do behaviourally subordinate species.

In social insects, self-organisation patterns emanate mainly from amplification processes that rely on positive feedback mechanisms (Deneubourg and Goss, 1989; Bonabeau et al., 1997; Detrain and Deneubourg, 2006). Regarding collective foraging, the keystone of amplification is recruitment. There are two kinds of recruitment mechanisms either direct or indirect (Beekman and Dussutour, 2009). In direct recruitment mechanisms, information are exchanged through direct interactions between individuals, such as dance in honey-bees (von Frisch, 1967), or tandem-running in ants (see 1.1.2). Indirect recruitment designates information transfer through modification of the environment as mass recruiting ants laying pheromone on the ground. Such recruitment systems are efficient even with poorly reliable individuals (Herbers, 1981). However, they can be altered by the environment. In foraging ants, the autocatalytic scenario depends on the use of trail pheromone: foragers are recruited by the pheromone trail that is reinforced by the successful foragers. Abiotic factors influence ant foraging behaviour both at the individual level, and by affecting the communication system. For example, foraging substrates influence collective choice (Detrain et al., 2001) by affecting both individual locomotion (Bernadou and Fourcassié, 2005) and pheromone decay (Jeanson et al., 2003). We focused on the effect of high temperatures. In chapters 6 & 7, we approach high temperatures as a disturbance of information transfer. Chapter 6 studies the contribution of high temperatures to the dynamics of information transfer between workers in a mass recruiting species, and chapter 7 compares the effect of high temperatures on the efficiency of chemical trails both at the behavioural and chemical level in a mass recruiting and a group recruiting species.

The decision whether to transmit information to nestmates is controlled by individual criteria based on local information and determines the group-level response (Detrain and Deneubourg, 2006). These individual choices are generally based on very simple rules. For instance, contact rates with nestmates might be a local cue acting as a signal to engage a specific task (Gordon, 1996; Bonabeau et al., 1998b; Greene and Gordon, 2007b). Regarding recruitment, the individual criteria to trail laying decision is based on an internal response threshold (Detrain and Deneubourg, 2002). If the forager is able to fill its crop (Mailleux et al., 2000) or is unable to move a prey on its own (Detrain and Deneubourg, 1997), it returns to the nest laying pheromone. At the colony scale, this generates state-dependant decisions. This kind of rule allows a regulation of the recruitment according to food source quality (de Biseau and Pasteels, 2000; Portha et al., 2002, 2004) or size (Detrain and Deneubourg, 1997, 2002; Cerdá et al., 2009), depending on the state of the colony such as the presence of brood (Portha et al., 2002, 2004) or the level of starvation (Mailleux et al., 2006). Ground temperature, like resource quality or competitor presence, might thus affect individuals in their binary choice whether to lay pheromone or not. Chapter 8 focuses on the foraging at high temperatures as a state-dependent decision, and chapter 9 briefly presents some concluding remarks about the previous studies.

CHAPTER 6

High temperatures affect trail efficiency through pheromone decay in ants [1], [2]

In Mediterranean habitats, temperature affects both ant foraging behaviour and community structure. Dominant species are generally less tolerant to high ground temperatures than subordinates. However, the mechanisms that constrain dominant species' foraging activity are not fully understood. Here we examined the effect of ground temperature on pheromone decay in Tapinoma nigerrimum. We hypothesised that high temperatures negatively affect the efficiency of chemical trails by accelerating pheromone evaporation. T. nigerrimum is a dominant ant species in Mediterranean communities. It uses a very efficient system of chemical trails to forage. Field observations showed that ground temperature variations underpinned the foraging activity pattern of this species. Under controlled conditions in the laboratory, we isolated the effect of raising temperature (from 25°C to 60°C) on the pheromone trail attractiveness in T. nigerrimum. An Y-shaped bridge with a branch previously marked by workers and an unmarked branch was presented to the experimental colonies. Both branches were heated and cooled down. Heating trail pheromone (marked branch of the bridge) without raising soil temperature affected the behavioural response of foragers regarding branch choice. High temperatures appeared therefore to reduce pheromone efficiency. We assessed the pheromone decays dynamics by a mechanistic model, whose parameters were fitted with Bayesian inference. A differential equation based on first principles described the dynamics of pheromone concentration. The model predicted ant's choice through the evolution of pheromone

---

[1] Co-authors: **E. Billoir, R. Boulay, C. Bernstein and X. Cerdá**

[2] Submitted to Functional Ecology

concentration on trails as a function of both temperature and time from pheromone deposition. Our results highlighted that the effect of high temperatures on recruitment intensity was partly due to pheromone evaporation. In the Mediterranean communities, this might affect dominant species, whose food collection mostly depends on collective foraging strategies relying on chemical communication, more than subordinate ant species, less dependent on chemical communication and less sensitive to high temperatures.

6.1 Introduction

In eusocial insects, workers foraging behaviour is expected to maximise the overall colony energy intake (Oster and Wilson, 1978). The total biomass of food retrieved by a colony directly results from the intensity and the duration of foraging activity (Cole et al., 2008). This foraging effort fluctuates both in the number of foragers involved and in the time they spend foraging (Cole et al., 2008). Temporal and spatial patterns of foraging activity are affected by both intrinsic and extrinsic factors (Hölldobler and Wilson, 1990). On the one hand, endogenous characteristics of the colony such as maturity (presence of brood, Portha et al. 2004; age of workers, Traniello 1989) or genetic background (Cole et al., 2010) might influence the foraging schedule. On the other hand, exogenous factors that include both biotic interactions such as predation (Whitford and Bryant, 1979), competition (Gordon, 1992; Brown and Gordon, 2000), or food availability (Bernstein, 1975; Brown and Gordon, 2000) and abiotic conditions such as microclimate (Marsh, 1985; Pol and Lopez de Casenave, 2004; Bucy and Breed, 2006; Azcárate et al., 2007; Chong and Lee, 2009) are expected to influence the foraging activity of many ant species.

In Mediterranean ecosystems, among the climatic variables that influence ant foraging, temperature is probably the most important (Azcárate et al., 2007). External temperatures are especially decisive for foraging activity since extreme temperatures affect the muscular control and survival of individuals (Cerdá et al., 1998a; Lighton and Turner, 2004; Maysov and Kipyatkov, 2009). In several ant communities, behaviourally dominant species that displace subordinate species at mild temperatures, are less tolerant to stressful temperatures (Cerdá et al., 1998a,c; Bestelmeyer, 2000). This dominance-thermal tolerance trade-off contributes to community structure promoting species coexistence (Retana and Cerdá, 2000; Lessard et al., 2009; Wittman et al., 2010). Temperature variations might thus reduce competitive exclusion through physiological differences between dominant and submissive species. In addition, competitive superiority is often linked to the use of chemical communication in territorial and foraging behaviour (Hölldobler and Carlin, 1987; Fellers, 1987; Savolainen and Vepsäläinen, 1988), and dominant species advantage might rely on the efficiency of their chemical communication.

Many ant species use chemical communication to exploit food sources efficiently (Hölldobler and Wilson, 1990). When a scout discovers a resource, it may lay a chemical trail while returning to the nest. Nestmates are attracted and orientated by this cue and guided to the resource. The chemical trail can be reinforced by each returning forager. The substance laid on the trail is a specific combination of chemical compounds (see Morgan 2009 for review). Trail pheromones are generally composed of relatively volatile, species-specific compounds. For instance, the trail pheromone of the ant *Tetramorium caespitum* L. is a mixture of two pyrazines (2,5-dimethylpyrazine and 3-ethyl-2,5-dimethylpyrazine, Attygalle and Morgan 1983). The rate at which the trail pheromone fades out may depend on temperature (as it occurs for sex pheromone McDonough et al. 1989; Ono 1993). However, to our knowledge, trail pheromone sensitivity to high temperature, and its consequence on recruitment efficiency has not been documented yet.

In this study, we analysed how foraging efficiency and trail-following behaviour vary according to temperature. We hypothesised that the high temperature sensitivity of trail-pheromones would constrain ant foraging activity. To test this hypothesis, we used a widespread Mediterranean ant species *Tapinoma nigerrimum* as a model system (Fig. 6.1). Previous studies have shown that this species uses mass recruitment with chemical trails (Cerdá et al., 1989). First, we analysed how foraging activity varies through the year and during the day as a function of ground temperature in the field. Second, we devised a laboratory experiment to test whether pheromone volatility limits ant recruitment in a range of temperatures found in nature. Third, we built a mechanistic mathematical model in order to explore the relationship between ant foraging activity and the rate of pheromone decay with temperature. In contrast with standard statistical models, our model was designed for a predictive purpose to allow a broader extrapolation on what occurs in nature out of the range of the studied values. Our approach, which is based on Bayesian inference of parameter estimates, is a flexible and powerful method especially when models involve multiple events, or dynamical processes (Ellison, 2004), as may be the case with workers recruitment during ant foraging.

6.2 Materials and methods

6.2.1 Model species and study sites

Tapinoma nigerrimum (Fig. 6.1) is a Mediterranean ant species, widespread in coastal areas (Bernard, 1983; Cerdá et al., 1989). Colonies are polygynous and polydomous, composed of extensive nests with many entrances inter-connected by above ground worker trails (Cerdá et al., 1989). Colonies are relatively populous with polymorphic workers (López et al., 1997) ranging from 2.5 to 5.1 mm length (Gomez and Espadaler, 1998). *T. nigerrimum* is an opportunistic species that mainly collects liquid resources such as aphid-honeydew or nectar, but also feeds upon dead insects (Cerdá et al., 1989, 1998b; Gomez and Espadaler, 1998). *T. nigerrimum* mainly adopts a collective foraging strategy by mass recruitment with chemical trails between the nest and food sources. The chemicals contained in the gaster of *T. nigerrimum* workers are identical to those of its twin species *T. simrothi* (see chapter 7 and Hefetz and Lloyd 1983) suggesting that *T. nigerrimum*'s trail pheromone is mainly composed of iridodials and iridomyrmecins (Simon and Hefetz, 1991).

Figure 6.1 — *T. nigerrimum* worker sipping *Euphorbia* sp. (photo: F. Amor)

Colony fractions of 1000-5000 workers were collected in the south of Spain (Doñana National Park, Huelva province; Sierra Nevada National Park, Granada province). They were reared in the lab in plastic boxes the bottoms of which were coated with plaster to maintain humidity. Small tubes with water and cotton wool also contributed to nest humidity. Room temperature remained constant at $25^oC \pm 1^oC$. Ants were fed three times a week with meal worms (*Tenebrio molitor*).

6.2.2 The effect of ground temperature on foraging activity

Data from a field study conducted previously in Canet de Mar (Barcelona, NE Spain) (Cros et al., 1997; Cerdá et al., 1997, 1998a) were re-analysed by focusing on the influence of temperature on the foraging behaviour of *T. nigerrimum* (for a detailed description of the study site, see Cerdá et al. 1989).

The foraging activity of *T. nigerrimum* was estimated from the number of foraging ants on the trails. The number of workers moving in both directions in a trail and crossing a mark (a line with a thread 2 cm high) was recorded for 3 min of each hour for 24 hours on 11 days between April and November (Cerdá et al., 1989). Together with the hourly measurement of activity at trail, ground surface temperature was measured with glass-headed thermocouples and a Univolt DT-830 multimeter.

Data were analysed by fitting generalized linear models (GLM) using the R software (R Development Core Team, 2010). The response variable was the number of ants on the trail. To take into account the auto-correlation due to the circadian rhythm, we modelled the daily cycle introducing as auxiliary independent variables: $H_{cos} = cos(2\pi\frac{\text{Hour}}{24})$, and $H_{sin} = sin(2\pi\frac{\text{Hour}}{24})$ as proposed in Crawley (2002). The other explanatory variables were the day of field observation (11-levels factor), the temperature (continuous), and their interaction. To deal with the overdispersion of data, we used a GLM with Quasi-Poisson error distribution. To give some flexibility to the effect of temperature on the response variable, we first introduced temperature effect as a third-degree polynomial. Non-significant effects were then progressively removed comparing the resulting scaled deviances with an F test.

6.2.3 The effect of temperature on trail following behaviour

The effect of temperature on pheromone persistence and ant ability to follow a trail was analysed in the lab (see Appendix 6.5.A). First (phase 1), a two-days fasting colony was connected to an unlimited food source (1:3 v:v honey:water) through a narrow (25×2×0.3 cm) glass bridge. During the next 30 min after the first ant started to explore the bridge, ants crossing the bridge (X) were counted during 1 minute every 5 minutes. We call initial efficiency (eff_0) the mean number of ants that crossed the bridge per minute during the first 30 minutes. In a second step (phase 2), the X glass bridge and a control, unmarked bridge (U) were maintained during 10 min at a given temperature (25, 30, 35, 40, 50 or 60°C). Both bridges were then cooled down during 5 min at room temperature (25°C). In the third step (phase 3), ants were offered access to both bridges. A Y-shaped device was constituted with the bridges X and U as the diverging branches, none of them leading to food. The location of both bridges (left or right side of the Y) was randomly chosen at each trial. The number of ants crossing either bridge during one minute was counted every 2 minutes during 30 min after the connexion of the bridges. Experiments were performed with four colony fragments, and two replicates per nest were conducted for each temperature.

We fitted two GLMs. In both cases, the response variable was the number of ants that crossed bridge X (success) and U (failure) during one minute. The first GLM tested whether or not temperature had an effect on the percentage of ants choosing bridge X in the first 10 min. Treatment temperature was considered as a categorical predictor variable to avoid assumptions on the shape of its effect. The significance of each level was tested by changing the contrast matrix. The second GLM aimed to identify the factors involved in the probability of choosing bridge X. The explanatory variables were the nest (4-levels factor), the initial efficiency (continuous), the temperature of treatment included as a continuous variable (continuity was justified by the first GLM), and the time elapsed since the connexion of the bridges (continuous). We used a GLM with a logit link function and a quasi-binomial error distribution. We built a full model that contained all variables and interactions between them. We progressively removed the non-significant effects until obtaining the most parsimonious model. Model selection was based on the comparison of the resulting scaled deviances with an F test.

6.2.4 The mechanistic model

Our mechanistic model aimed at specifying the nature of the relationship between temperature and the probability of choosing a branch in a dynamic process. We estimated model parameters using Bayesian inference with the data of the previous experiment.

Firstly, for each experimental replicate j ($j \in [1, 48]$), we assumed the initial efficiency eff_j to be an estimate of the initial pheromone concentration (phase 1). Then, we suggested that the concentration of pheromone on a branch $C_{t,j}$ is a function of the initial concentration eff_j, and the time elapsed at the different temperatures. As in previous studies on pheromone evaporation, we assumed an exponential decay of the trail pheromone concentration (Beckers et al., 1993; Jeanson et al., 2003).

$$C_{t,j} \;=\; \text{eff}_j \, e^{-\alpha t} \tag{6.1}$$

where α is the inverse of the mean lifetime of the trail pheromone. It might be considered as the evaporation velocity of the chemicals. According to the kinetic theory of gases commonly used to model biological processes (Gillooly et al., 2001; Brown et al., 2004), the average molecular kinetic energy is proportional to the absolute temperature (in degrees K) ($< \frac{1}{2}mv^2 > = \frac{3}{2}k_B T$, where k_B is Boltzmann's constant, m and v are respectively the mass and the velocity of the particle, and T is the absolute temperature). The velocity of each particle is hence proportional to the square root of the absolute temperature. We assumed that the evaporation velocity of the pheromone depends likewise on the temperature: $\alpha = \beta\sqrt{T + T_{ref}}$, with β and T_{ref} being constants specific to the pheromone composition. Note that particular units used to express temperatures do not matter provided that T_{ref} and T are expressed on the same scale. We used Celsius degrees. So, we explicited equation (6.1):

$$C_{t,j} \;=\; \text{eff}_j \, e^{-\beta t \sqrt{T + T_{ref}}} \tag{6.2}$$

In our experiment, pheromone decayed differently during the last two phases. During phase 2, the bridges were exposed during 10 min (t_h) at the experimental temperature (T).

The remaining concentration after this phase is thus $C_{0,j} = \text{eff}_j e^{-\beta t_h \sqrt{T+T_{ref}}}$. During the test (phase 3), bridges were exposed i min at room temperature ($T_e = 25°\text{C}$). Pheromone concentration is thus $C_{i,j} = C_{0,j} e^{-\beta i \sqrt{T_e+T_{ref}}}$.

The amount of pheromone on a branch determines the probability of choosing a given branch in a two branches choice. Deneubourg et al. (1990) suggested the following function to quantify the probability of choosing branch X, $prob(X)$, given two branches X and U.

$$prob(X) \ = \ \frac{(k+N_X)^n}{(k+N_X)^n \ + \ (k+N_U)^n} \tag{6.3}$$

N_X (resp. N_U) represents the number of ants that previously passed on branch X (resp. U). Parameter n determines the degree of non-linearity of the choice, e.g. a high value of n means that even slight differences between branches lead to high probability of choice. Parameter k corresponds to the degree of attraction attributed to an unmarked branch.

The number of ants that passed on a branch is an estimate of the pheromone concentration on this branch. In our system, no ant passed on bridge U ($N_U = 0$) and the pheromone concentration on bridge X, at time i, is $C_{i,j}$. Equation (6.3) becomes:

$$prob(X)_{i,j} \ = \ \frac{(k+C_{i,j})^n}{(k+C_{i,j})^n \ + \ k^n} \tag{6.4}$$

We assumed that the effective number of ants choosing bridge X ($X_{i,j}$) was a realisation of a binomial function with success probability $prob(X)_{i,j}$ and $Tot_{i,j}$ trials, where $Tot_{i,j}$ is the total of ants coming out of the nest at time i for replicate j.

To estimate the parameters of the mechanistic model, we used Bayesian inference. All parameters were considered as unknown random variables with non-informative prior probability distributions (Appendix 6.5.B). Bayesian inference consists in updating from chosen prior probability distributions to posterior probability distributions given the data (Spiegelhalter et al., 1996; Ntzoufras, 2009). Practically, Bayesian inference was performed using Markov Chains Monte Carlo (MCMC) algorithms with the *rjags* R package (Plummer, 2009). Some details on the inference are provided in Appendix 6.5.B. Implementation code is available upon request to the authors.

When attempting to estimate simultaneously the four parameters involved in the proposed mechanistic model, according to the Gelman and Rubin diagnostics (Gelman and Rubin, 1992; Brooks and Gelman, 1997), the Bayesian algorithm failed to reach convergence. This was due to strong correlation between parameters, which suggested overparameterization of the model. To reduce the number of parameters to estimate, we tested the values proposed by Deneubourg et al. (1990) on the basis of an empirical fitting: $k \approx 20$ and $n \approx 2$. Hence, we fitted three simplified models, by fixing respectively k, n or both. In these three cases, the convergence of the estimation process was successful. We then relied on the DIC (Deviance Information Criterion, Plummer 2008) to identify the best model.

6.3 Results

6.3.1 The effect of ground temperature on foraging activity

Temperature had a significant non linear effect on the foraging activity of *Tapinoma nigerrimum* depending on both the hour of the day and the day of the year. The best statistical model included the effect of the hour, the day, and temperature as a quadratic function (Table 6.2). Daily variations explained part of the variability in foraging activity fluctuations. The endogenous circadian oscillations represented by the two variables H_{sin} and H_{cos} also had a significant influence. Even taking into account the circadian rhythm, the relation between foraging activity and ground temperature followed a parabola. For low temperatures (<25°C), raising temperature increased foraging activity whilst the opposite was registered for high temperatures (>30°C). However, significant interactions between the day and both temperature and squared temperature revealed that the exact shape of the parabola varied between days with maximum activity ranging between 18 and 30°C. Among the 11 days some showed similar patterns and could be regrouped into 7 day-groups (Fig. 6.3). For 5 day-groups (day-group A: 20/04, day-group C: 01/06 and 01/07, day-group D: 13/07, 24/07 and 07/08, day-group E: 21/08 and day-group G: 04/11), temperature was a good predictor of foraging activity. However, for day-groups B (19/05) and F (16/09 and 14/10), temperature effect was not significant.

Table 6.2 — The influence of ground temperature, circadian rhythm and day of observation on the foraging activity of *T. nigerrimum* (number of ants on trails). Analysis of Deviance Table of the selected GLM (family: quasipoisson, link: log, Response: Number of ants). Terms were added sequentially (first to last).

Effect	Df	Resid. Df	F	P-value
H_{sin}	1	240	31	<0.001
H_{cos}	1	239	222	<0.001
Day-group	6	233	97	<0.001
Temperature	1	232	154	<0.001
Temperature^2	1	231	174	<0.001
Day-group:Temperature	6	225	9	<0.001
Day-group:Temperature^2	6	219	4	0.001

H_{sin} and H_{cos} refer to the daily variations (see 6.2).

Day-group represents the seasonal variations (group of days in different period of the year).

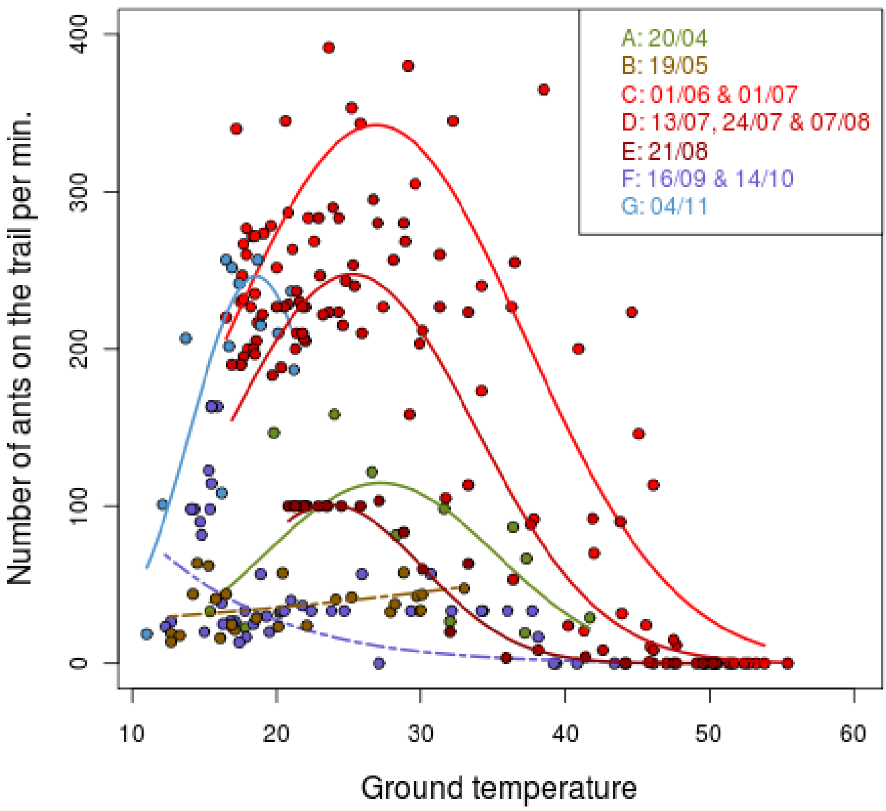


Figure 6.3 — The number of *T. nigerrimum* foragers on a trail, in field conditions, according to ground temperature. Field observations (points) and GLM predictions (lines). Dot-dashed lines stand for non-significant temperature effects. Colours differentiate day groups from April to November (see insert)

6.3.2 Temperature effect on trail following behaviour

Treatment temperature had a significant effect on ants first choice ($F_{5,234} = 35$, p<0.001). During the first 10 min, ants chose preferentially bridge marked (X) after temperature treatments lower than 40°C but failed to discriminate between bridges after higher treatment temperatures (Fig. 6.4). However, the only significant difference between two adjacent temperatures was between 25°and 30°(t= 3.213, p=0.002). The effect of temperature on choosing probability was rather progressive (Fig. 6.4), what made more appropriate the consideration of temperature effect as a continuous variable.

The analyses of ant choice variation across time specified the effect of different variables on the persistence of trail pheromone. The most parsimonious GLM included the effect of the logarithm of the temperature of treatment, the time elapsed, the initial efficiency (eff_0), the

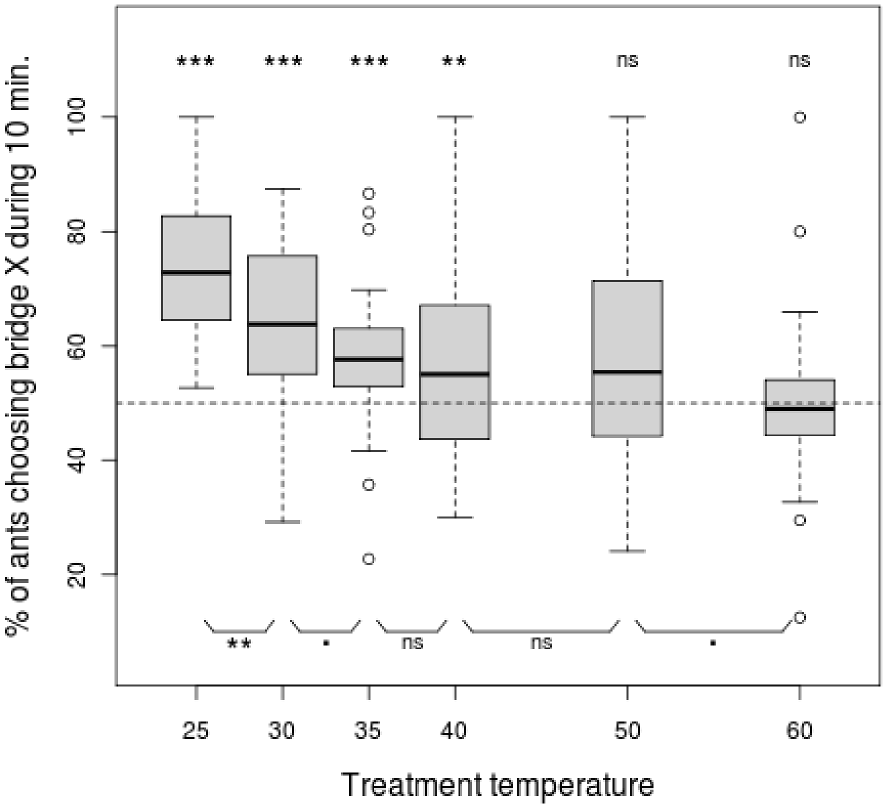


Figure 6.4 — Proportion of *T. nigerrimum* workers choosing the previously marked bridge as a function of the temperature treatment. The box plot groups data for all nests and time since the start of the experiment lower than 10 min. Temperature effect is estimated from the GLM by changing the contrast matrix. The significance of choice probability for each temperature is indicated above the boxes. Differences between two treatments in the probability of choosing are represented at the bottom of the plot. (*** = $p < 0.001$, ** = $p < 0.01$, * = $p < 0.05$, . = $p < 0.1$, ns = $p > 0.1$)

group of nests (nests have been reduced without loss of precision to a two-levels factor), the interaction between temperature and time, and the interactions of eff_0 with temperature, time and nest (Table 6.5). The higher the treatment temperature, the weaker was the preference for bridge X. Time passed since the connection of the Y-shaped device also had a significant negative effect on ants' choice (Table 6.5). The positive interaction between temperature and time effect prevented the under-estimation of the choosing probability for high temperature and time values. For high values of eff_0, the decrease in ants' choosiness due to increases in temperature and time elapsed was higher. The response varied between nests, but the coupled effect of temperature and time was independent of nest (Table 6.5).

Table 6.5 — Choice between a pheromone marked or unmarked bridge in a Y shaped device, as a function of treatment temperature, initial efficiency, nest group, and time elapsed since the connection of the bridges. Estimation of each variable in the linear predictor of the GLM with `quasibinomial` family. Dispersion parameter for quasibinomial family is taken to be 1.85

	Estimate	Std. Error	t value	p value
Nest (group 1)	3.735	0.507	7.374	<0.001
Nest (group 2)	4.576	0.522	8.769	<0.001
Efficiency (group 1)	0.027	0.008	3.328	<0.001
Efficiency (group 2)	0.011	0.009	1.294	0.196
Time	-0.080	0.021	-3.895	<0.001
log(Temperature)	-1.038	0.142	-7.335	<0.001
Efficiency:Time	-0.0002	0.00008	-2.348	0.019
Efficiency:log(Temperature)	-0.004	0.002	-1.999	0.046
Time:log(Temperature)	0.022	0.006	3.830	<0.001

6.3.3 The mechanistic model

The minimum DIC was obtained for the simplified model fixing k at 20 and the parameters were estimated as (median [95% CI]) T_{ref} = -24.56 [-24.74; -24.34], β = 0.059 [0.053; 0.065] and n = 1.17 [1.01; 1.33]. To check the goodness-of-fit of the mechanistic model, we compared observed and corresponding predicted data as shown xin Appendix 6.5.B. (Fig. 6.9). All observed values of X were reasonably predicted by the model with no clear outlier. The three simplified models led to not significantly different β estimates (0.056 [0.051; 0.062] when fixing n and 0.064 [0.059; 0.070] fixing both k and n), and to close T_{ref} estimates (-24.46 [-24.66; -24.20] fixing n and -23.74 [-23.98; -23.46] fixing k and n).

The model allows predicting the dynamics of pheromone concentration, a process difficult to access experimentally. The predictions concern both the time-course of pheromone concentration depending on temperature (Fig. 6.6, lower part), and its direct influence on ants path choice (Fig. 6.6, upper part). The good adequacy of our model (Appendix 6.5.B) allows to rely qualitatively on the predictions and suggests that the key processes involved were accounted for.

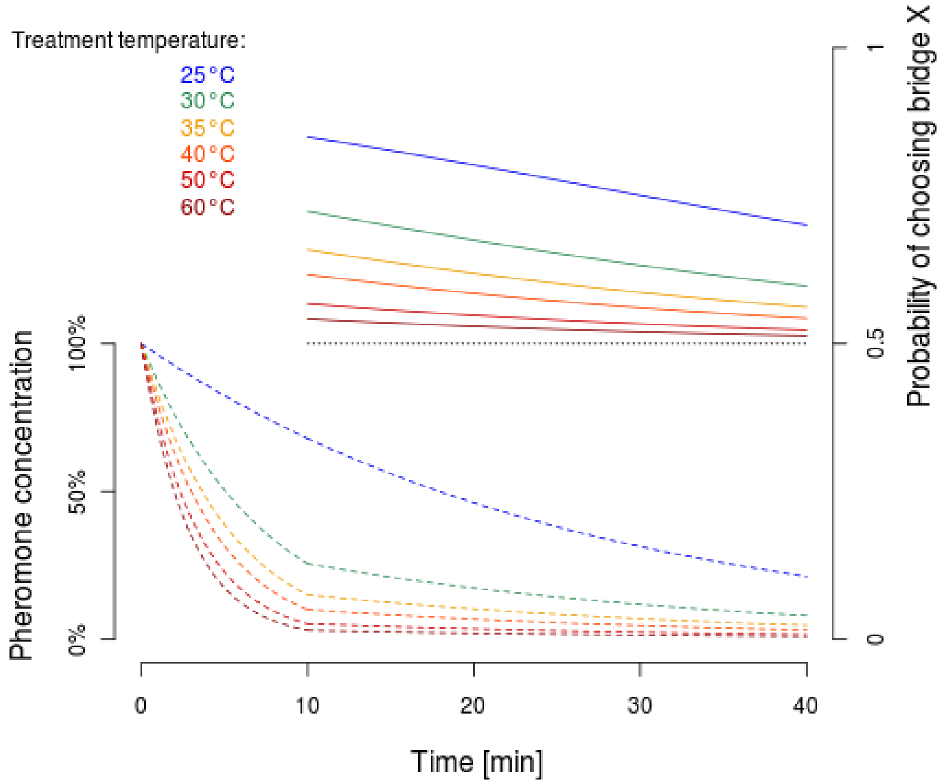


Figure 6.6 — Pheromone decay and its influence on ants choice as predicted by the mechanistic model. Lower panel: estimation of the pheromone concentration on the marked branch of a Y shaped device. Upper panel: probability of choosing the marked bridge.

6.4 Discussion

The present study shows the importance of temperature on the recruitment behaviour in ants. Field observations highlighted the effect of temperature on the shape of foraging activity. Behavioural assays demonstrated that the rate of pheromone decay depended on temperature. The nature of the dependence was successfully assessed by a mechanistic model.

The field results demonstrated that, as expected, *T. nigerrimum* foraging activity highly depended on ground temperature both at the daily and seasonal scales. In natural conditions, the shape of recruitment intensity according to temperature was unimodal. The peak of maximal activity estimated at 24°C in a previous study (Cerdá et al., 1998a) varied throughout the year between 18°C in November and 30°C in June. This seasonal difference in temperature preference might be controlled by the interaction with other abiotic factors such as atmospheric pressure, humidity, or light radiation (Marsh, 1985; Azcárate et al., 2007; Chong and Lee, 2009), or by the variation of biotic environment such as resource availability, competition, or predation pressure (Brown and Gordon, 2000; Wittman et al., 2010). The intrinsic state of the colony, dependent on the reproductive cycle of the species, might also be an essential factor influencing both the needs and the foraging ability (number and age of workers) of the colony (Hölldobler and Wilson, 1990). However, in spite of the variation in seasonal preferences, ground temperature remained a good predictor of surface activity in *T. nigerrimum*.

The behavioural assays on branch choice clearly showed that high temperatures accelerated pheromone decay, probably through the evaporation or degradation of its components. High temperature affected trail pheromone orientation function. Other abiotic factors such as the foraging substrate also influence recruitment efficiency (Jeanson et al., 2003). Unfavorable environmental conditions might thus be essential in collective foraging processes since they affect chemical communication between foragers. This modification of the information transfer interplays with an amplification of individual preferences. Indeed, regarding high temperatures, the direct effect on ants physiology is essential (Hölldobler and Wilson, 1990). In Mediterranean environment, hot temperatures might eventually represent a mortality risk (Cerdá et al., 1998a). The effect of temperature on foraging patterns might thus result from the interplay between individual physiology and pheromone decay. In mass recruiting species, pheromone stability might thus have co-evolved with ants thermal tolerance. Indeed, in species commonly feeding on stable resources, such as *T. nigerrimum* that exploits aphid honeydew, pheromone persistence is essential to foraging efficiency. In this species, if the pheromone is sensitive to high temperature, the costly synthesis of heat shock proteins necessary for thermotolerance (Gehring and Wehner, 1995) would not be adaptive.

Our mechanistic model allowed to assess pheromone functionality from ants behaviour. The simple mechanism we suggested (equation 6.2) described the contribution of high temperatures on pheromone decay. We linked pheromone evaporation to ants choice with the reference model of Deneubourg et al. (1990). Our model could be parametrised by Bayesian inference on experimental data, making predictions reliable. Moreover, our Markov Chain Monte Carlo (MCMC) method raised an interesting point about the path choice model of Deneubourg et al. (1990). This model provides an accurate description of ants choice given the intensity of the chemical signal. Practically, ants' preferences depend on pheromone concentration and two parameters that control the choice linearity. When running iterations to estimate parameters by Bayesian inference, these two parameters appeared positively correlated. The higher the concentration threshold for trail efficiency, the higher the pheromone sensitive choice. Besides, our estimates were rather different from the values obtained when fitting the exploratory behaviour of the Argentine Ant *Linepithema humile* (Deneubourg et al., 1990) ($n \approx 2$, $k \approx 20$) or the recruitment trail of *Lasius niger* Beckers et al. (1993) ($n \approx 2$, $k \approx 6$). We estimated a lower degree of choice nonlinearity (fixing $k = 20$, $n \approx 1.17$; fixing $n = 2$, $k \approx 39.59$). Theoretically, low nonlinearity suggests a poor ability to select the best food source (Nicolis et al., 2003). Nevertheless, since *T. nigerrimum* displayed good trail following proficiency, the difference might rather rely on a divergence of experimental procedures. Indeed, they differed on many aspects from the measure of initial pheromone concentration to the starvation state of the colonies (Hangartner, 1969).

At the community level, differences between ant species thermal tolerance is often invoked to explain species coexistence (Cerdá et al., 1998a,c; Bestelmeyer, 2000; Lessard et al., 2009; Wittman et al., 2010). *T. nigerrimum* is a dominant species (Cerdá et al., 1997; Blight et al., 2010). In Mediterranean ant communities, behaviourally dominant species are less tolerant to high temperatures, and thermal stress might even disrupt the expected dominance hierarchy (Cerdá et al., 1997). As behavioural dominance is closely linked to numerical dominance (Savolainen and Vepsäläinen, 1988; Davidson, 1998), competitive superiority might depend on the recruitment process. A loss in recruitment efficiency might thus affect the competitive capacity thereby contributing to the disruption of dominance hierarchy at high temperatures. Moreover, in some species the same compounds cause both recruitment and alarm behaviour. For instance, in *T. simrothi*, closely related to *T. nigerrimum*, the same exudate is used for both trail-following and defensive behaviour according to its concentration although the concentration threshold to induce alarm behaviour is much higher (about 10 times) than for trail-following (Hefetz and Lloyd, 1983; Simon and Hefetz, 1991). Very high pheromone concentrations might thus be necessary to evoke in ants a high level of aggression. If high temperatures affect pheromone concentration as we show here, it might be very difficult to trigger ants aggressiveness when soil is hot. On the other hand, subordinate species use other foraging strategies less dependent on chemical communication (e.g. group-recruitment, or individual foraging) and are less sensitive to high temperatures (Ruano et al., 2000). Therefore, their foraging efficiency remains unaffected by high temperature. So, in Mediterranean communities where temperature shows important seasonal and daily variations, the pheromone thermal decay affects preferentially dominant species, and can be considered as one of the mechanisms ensuring the persistence of the inferior competitors.

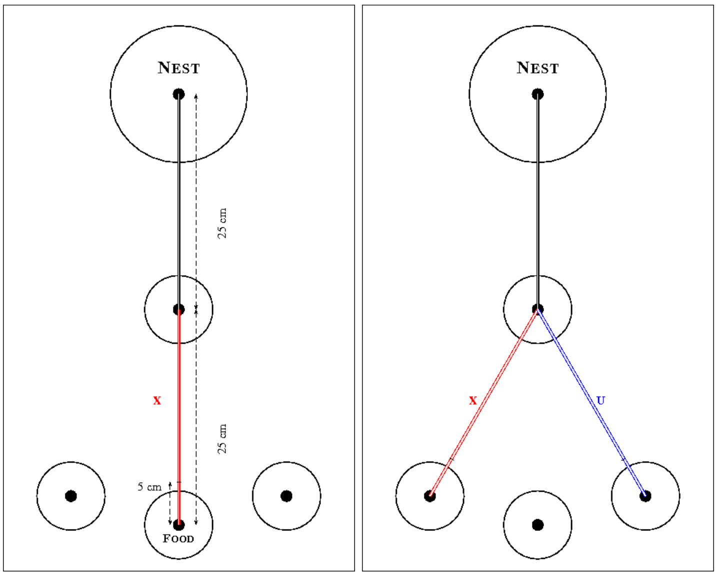
To conclude, our study provides experimental evidence of the effect of high temperatures reducing trail pheromone efficiency. The behavioural response of foraging ants regarding daily and seasonal variations in temperature might thus be partly assigned to pheromone decay. Foraging ants are affected by high temperatures both at a physiological level, and in their communication system. The value of our mechanistic model is to enable explicit quantitative predictions based on first principles. It is particularly adapted to the experimental setting we developed where ants were not exposed to high temperatures but trail pheromone was.

Acknowledgements

We are very gratefull to Alain Lenoir for his early review of this manuscript. We thank Javier Retana, Jordi Bosch, Sebastià Cros and Anna Alsina who provided the field data. Experimental work in EBD have been funded by Spanish Ministerio de Ciencia e Inovación (project CGL2009-09690/BOS). Thanks are due to Jean-Philippe Lessard and Ana Carvajal who helped during field ant collection. Doñana National Park and Sierra Nevada National Park authorities gave permission to collect ant colonies.

6.5 Appendix

6.5.A Y-shaped device



(a) (b)

Figure 6.7 — Scheme of the experimental design. (a) Phase 1: pheromone deposition on bridge X. (b) Phase 3: Y-test on pheromone persistence next to warming treatment.

6.5.B Bayesian Inference

A Bayesian model is specified by a set of prior distributions, and a set of hierarchical conditional links (deterministic or stochastic) from parameters to data (Fig. 6.8). In our case, the processes described in the model formalism constituted stochastic links (System 6.5):

$$\begin{aligned} C_{0,j} &= \mathrm{eff}_j \; e^{-\beta t_h \sqrt{T+T_{ref}}} \\ C_{i,j} &= C_{0,j} \; e^{-\beta i \sqrt{T_e+T_{ref}}} \\ \mathbb{P}_{i,j} &= \frac{(k+C_{i,j})^n}{(k+C_{i,j})^n \; + \; k^n} \end{aligned} \tag{6.5}$$

Data were then related to the model output assuming a binomial error model:

$$X_{i,j} \sim \mathcal{B}in(\mathbb{P}_{i,j}, Tot_{i,j})$$

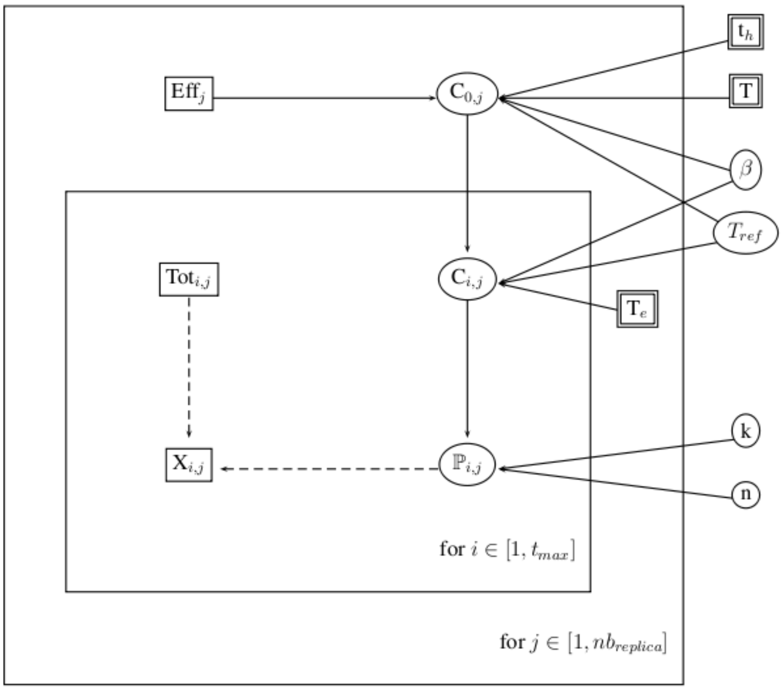


Figure 6.8 — Graphical representation of the mechanistic model. Data are denoted by rectangles, covariates by double-rectangles, and the other nodes (parameters, variables) by ellipses. Solid arrows indicate deterministic links while dashed arrows indicate stochastic links. For each replicate j, Eff$_j$ is the initial efficiency; $C_{0,j}$ is the concentration after passing t_h (fixed at 10 min) minutes at T°C; $C_{i,j}$ is the concentration after passing i minutes at T_e°C (fixed at 25°C). $\mathbb{P}_{i,j}$ is the probability of choosing the previously marked bridge, Tot$_{i,j}$ is the number of ants passing on one of the two bridges, and X$_{i,j}$ is the number of ants passing on the marked bridge between time $i-1$ and time i. β, T_{ref}, k and n are estimated by the model.

As priors, we chose large non-informative distributions, only bounding parameters in their possible interval when necessary. T_{ref} was bounded upon -25°C to ensure the well-definition of $\sqrt{T + T_{ref}}$, and β, n, and k were assumed to be positive. Hence, we used the following priors: $T_{ref} \sim \mathcal{U}nif(inf = -25, sup = 1000)$, $\beta \sim \mathcal{U}nif(inf = 0, sup = 1)$, $n \sim \mathcal{U}nif(inf = 0, sup = 10)$ and $k \sim \mathcal{G}amma(shape = 0.001, rate = 0.001)$.

Three independent Markov Chain Monte Carlo (MCMC) chains were run in parallel. After an initial burn-in period of 5,000 iterations, the Bayesian algorithm was run 10,000 iterations and the corresponding sample of parameter posterior distributions were recorded. Also data predictions were simulated and recorded for posterior predictive checking of the proposed modelling. In contrast to a data/model fitting representation, posterior predictive checking also takes into account the chosen error model (Fig. 6.9).

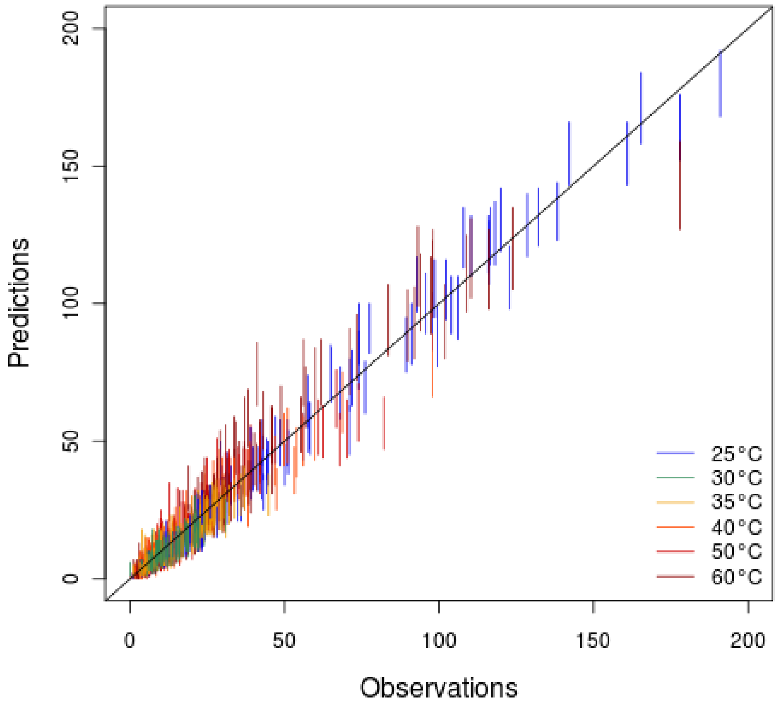


Figure 6.9 — Posterior predictive checking of the mechanistic model: comparison of the predicted number of ants on the pheromone marked bridge as a function of the values observed. The predictions are shown as segments corresponding to their 95% credible intervals. The colours corresponding to the different temperatures are indicated in the figure.

CHAPTER 7

From ant behaviour to pheromone decay: does the effect of high temperatures differ according to the recruitment strategy? [1]

Many ant species use pheromone to communicate resource location to nestmates. Mass-recruiting species lay long-lasting anonymous chemical trails while group-recruiting species use temporary chemical trails. We studied how high temperature influenced the foraging behaviour of a mass-recruiting species (Tapinoma nigerrimum) and a group-recruiting species (Aphaenogaster senilis). We first showed that the foraging activity dependence on temperatures was stronger for mass-recruiters than for group-recruiters in the field. Then, under controlled conditions, we isolated the effect of raising temperature (from 25°C to 55°C) on the trail pheromone of both species. On the one hand, heating trail pheromone without raising soil temperature affected the behavioural response of the mass-recruiters more than the choice of the group-recruiters. On the other hand, chemical analyses of the pheromone under the same temperature treatments showed that the mass-recruiters pheromone was more stable to high temperature than the group-recruiters pheromone. Our results suggest that mass-recruiting species invest more in communication efficiency than group-recruiting species. However, since the latter was less affected by pheromone evaporation at the behavioural level, group-recruitment might be an adaptation to variable environment with fluctuating temperatures.

---

[1] Co-authors: **A. Lenoir, R. Boulay, C. Bernstein and X. Cerdá**

7.1 Introduction

At the community level, the foraging strategy is often considered to be linked to the competitive ability of the species. Species able to increase rapidly their abundance at a given food source might have an advantage to displace competitors (Fellers, 1987; Savolainen and Vepsäläinen, 1988; Andersen, 1992; Cerdá et al., 1998a). Competition is identified as the "hallmark of ant ecology" (Hölldobler and Wilson, 1990) and structures many ant communities in a dominance hierarchy (Andersen, 1992; Parr et al., 2005). The behaviourally dominant species competitively exclude the subordinate species (Fellers, 1987; Savolainen and Vepsäläinen, 1988; Perfecto, 1994; Sanders and Gordon, 2003). A key question therefore is the understanding of the factors enabling species coexistence in the same community (Andersen, 2008). Niches partitioning is a well-known mechanisms reducing interferences (Savolainen and Vepsäläinen, 1989; Hölldobler and Wilson, 1990; Albrecht and Gotelli, 2001). Co-occurring species might differ in their nesting requirements (Torres, 1984) and in their diet (Cerdá et al., 1998b; Sanders and Gordon, 2003; Blüthgen and Fiedler, 2004; Lebrun, 2005). Dominant and subordinate species often present different foraging schedules (Savolainen and Vepsäläinen, 1989; Hölldobler and Wilson, 1990; Cros et al., 1997; Retana and Cerdá, 2000). In Mediterranean communities for instance, during the hot summer days, dominant species tend to forage at night while subordinates are more abundant during the day (Cros et al., 1997). This temporal segregation might reflect the different thermal preference of the species.

In ants, feeding habits vary in their individual and social components (Traniello, 1989). Although a few species forage individually without communicating food location to nestmates (e.g. *Cataglyphis cursor*, Lenoir et al. 1990), the great majority of ants rely on recruitment to exploit food ressources (Wilson, 1971). Recruitment processes might involve a combination of different cues from touch, stridulation and pheromones (Hölldobler and Wilson, 1990). In many species, an exploring ant (or scout) that has discovered a food source lays a pheromone trail in order to share information with her nestmates about the food source location. This pheromone trail both attracts and orientates nestmates to the food source, and the recruits become recruiters. Recruitment behaviour can be classified according to the increasing level of communication complexity it requires (Wilson, 1971; Beckers et al., 1989). In group recruitment a scout lays a trail that guides a small group of foragers (e.g. *Camponotus socius* Hölldobler, 1971; Kohl et al., 2001). This strategy involves a leader, contrary to chemical mass-recruitment (Bonabeau et al., 1998a). Mass-recruitment implies independent trail-laying and trail-following behaviour (e.g. *Lasius niger* Beckers et al. (1992)). Both group and mass recruitment allow the adjustment of the collective response to a given environment (Detrain and Deneubourg, 2002; Cerdá et al., 2009). On the one hand, group recruitment permits the exploitation of a wider range of food items (Cerdá et al., 2009). On the other hand, mass recruitment is more efficient for long-lived resources since it allows the rapid recruitment of a huge number of nestmates (Jaffe, 1980).

Temperature is an essential dimension of what Hölldobler and Wilson (1990) calls the "temperature-humidity envelope" that determines the microenvironment favorable to the foraging activity of ant species. In many communities, subordinate species tend to be more tolerant to stressful temperatures (Cerdá et al., 1998a; Bestelmeyer, 2000; Lessard et al., 2009; Wittman et al., 2010). In Mediterranean communities, some subordinate species even show some behavioural (gaster raising in *Cataglyphis rosenhaueri* makes a difference til 6.5°C Cerdá and Retana 2000), morphological such as worker polymorphism (larger workers are less subject to dessication Lighton and Feener 1989) and biochemical (heat shock proteins synthesis Gehring and Wehner 1995) adaptations to arid environments (Cerdá and Retana, 2000; Lenoir et al., 2009). Subordinate species might have experienced character displacement to adapt to thermally stressful environments like Mediterranean ecosystems where temperatures fluctuate both daily and seasonally. Nevertheless, one could wonder what would be the constraints on dominant species that prevent such thermal tolerance to evolve. Since dominance is linked to the efficiency of the recruitment process to control food source against competitors, we hypothesized that the foraging strategy could be such a constraint.

In a previous study, we showed that temperature negatively affected trail pheromone in a dominant mass recruiting species (chapter 6). In this study we aim to understand whether high temperatures affected differently the foraging activity of ant species according to their foraging strategy. We expected that mass recruiting species would be more sensitive to high temperature than group recruiting species. In particular, we presumed that the pheromone used by group foraging species would be more resistant to high temperatures. To test this hypothesis, we used two common ant species in Mediterranean communities as model system. The dominant *Tapinoma nigerrimum* represented the species using mass-recruitment (Cerdá et al., 1989) whereas the more subordinate *Aphaenogaster senilis* exemplified the group foraging species (Cerdá et al., 2009). To grasp the overall effect of high temperatures on the foraging behaviour of these two species, we addressed the following questions: i/ Is *T. nigerrimum* and *A. senilis* foraging activity similarly affected by temperature variations in the field? ii/ Is their trail-following behaviour identically affected by the exposition of their trail-pheromone to high temperature? iii/ Is the chemical composition of their pheromone equally altered by high temperatures?

7.2 Materials and methods

7.2.1 Model species and studied sites

Our model species were two widespread Mediterranean ant species: *Tapinoma nigerrimum* (Nylander) (Fig. 6.1) and *Aphaenogaster senilis* (Mayr) (Fig. 7.1). *T. nigerrimum* is a highly polygynous and polydomous, dominant species that form extremely populous societies (Cerdá et al., 1989, 1997). Workers collect mainly aphids honeydew, but also feed on arthropod corpses (Cerdá et al., 1989). They use mass recruitment with relatively long-lasting chemical trails between the nest and the food source (Cerdá et al., 1989). Their pheromone originates from the pygidial gland in the gaster (Pavan and Trave, 1958; Simon and Hefetz, 1991). By contrast, *A. senilis* is a strictly monogynous, monodomous, subordinate species, the colonies of which contain on average 1300 workers (Boulay et al., 2007b). It is an opportunistic omnivorous species that feed on dead arthropods and a variety of vegetal items including petals and seeds (Boulay et al. (2007b); Barroso, unpublished data). They use group-recruitment when food items are not transportable (Cerdá et al., 2009). To recruit nestmates, *A. senilis* workers secrete an alkaloid and hydrocarbon based pheromone from abdominal glands including the Dufour and venom glands (Lenoir et al., *In prep.*).

Figure 7.1 — *Aphaenogaster senilis* worker carrying a petal (photo: F. Amor)

The field study was conducted previously in Canet de Mar (Barcelona, NE Spain) (Cros et al., 1997; Cerdá et al., 1997, 1998a) (for a detailed description of the study site, see Cerdá et al. (1989)).

For laboratory studies, ants were collected in the south of Spain (Doñana National Park) and transferred to artificial nests. For *A. senilis* , experimental units were medium size queenright colonies (1000 workers and abundant brood). For *T. nigerrimum* , experimental units were colony fragments (1000-5000 workers) with one or several queens. We disposed of 6 artificial colonies for each species. Artificial nests were plastic boxes the bottoms of which were coated with plaster to maintain humidity. Small tubes with water and cotton also contributed to maintain nest humidity. Room temperature and humidity remained constant at 25 °C ± 1°C and 35% ± 5% respectively. Ants were fed three times a week with meal worms (*Tenebrio molitor*). Experiments were conducted on two days fasting colonies.

7.2.2 The importance of temperature on ant foraging

Foraging activity was recorded in the field each hour for 24 hours for 11 days (from April to November) (Cerdá et al., 1989). For *T. nigerrimum* , the foraging activity was the number of workers crossing a mark in a trail (in any direction) for 3 min. For *A. senilis* , the foraging activity was the number of workers entering or leaving the nest for 10 min (summed for two nests). Ground surface temperature was measured each hour with glass-headed thermocouples and a Univolt DT-830 multimeter.

All statistical analyses were performed using the R software (R Development Core Team, 2010). We started by modelling the seasonal and daily component of foraging activity for both species. In this purpose, we first fitted a generalized linear model (GLM) with `quasipoisson` family. The response variable was the foraging activity. To deal with seasonal variability, the day of sampling (11-levels factor) and its interaction with the species were introduced as explanatory variables. To take into account the variability due to the circadian rhythm, we modelled the daily cycle introducing as auxiliary independent variables: $H_{cos} = cos(2\pi\frac{\text{Hour}}{24})$, and $H_{sin} = sin(2\pi\frac{\text{Hour}}{24})$ as proposed in Crawley (2002). H_{cos} and H_{sin} estimated for each species were also introduced as explanatory variable of this first GLM. To test whether temperature could explain part of the variability of foraging activity, we fitted a linear model on the residuals of the first GLM. Explanatory variables were the temperature introduced as a third degree polynomial, the species, the day of sampling, and interactions. Non-significant effects were progressively removed, and non-significant levels of the day variable on temporally successive days were reduced.

7.2.3 Pheromone identification

In order to identify the trail pheromone of *Tapinoma nigerrimum* , we analysed the composition of abdominal secretions. 10 to 20 ants were extracted in hexane. The extract was concentrated to 100 μL under nitrogen flow and 2 μL were injected into a Perkin-Elmer GC-MS operating at 70EV with a DB-5 fused silica capillary column (length 30m, inner diameter 0.25mm, and film thickness 0.10 μm). The temperature program started at 50°C for 5 min, then raised to 150°C at 5°C.min^{-1}, to 320°C at 15°C.min^{-1}, and held at 320°C for the last 5 min. This program and the use of the gasters enabled to separate substances in two parts, the first one with volatile compounds (supposed to come from the pygidial (anal) gland like in T. simrothi as described by Simon and Hefetz (1991)) and the second part for non-volatile cuticular hydrocarbons. The data of 12 replicates were analysed to obtain the relative chemical composition of gaster extracts. In addition, for 9 extracts, an internal standard was added to determine the quantity of compounds per individuals.

The trail pheromone of *Aphaenogaster senilis* has been studied elsewhere (Lenoir et al., *In prep.*): it is formed by the secretion of two glands: Dufour gland and poison gland. The Dufour gland contains mainly hydrocarbons (Boulay et al., 2007b) while the poison gland contains a lot of alkaloids (Lenoir et al., *In prep.*). Therefore, we simply verified that the profiles of our experimental colonies were identical to those previously described for the species.

7.2.4 The effect of high temperatures on ant behavioural response

Gaster secretions were obtained by excising the gaster of 20 chilled ants (see Appendix 7.5.A, Fig. 7.11) and then extracted 24 hours with 400μL hexane. This extract was then diluted to obtain the different concentrations (1:1, 1:10, 1:100 v:v extract:hexane). Experiments were led every days with fresh extract.

The aim of this experiment was to test whether i/ temperature had an effect on the pheromone persistence and the ability of ants to follow an artificial trail with different dilutions, and ii/ the effect was different between the two model species. First, a trail of 10μL of the gaster extract was laid artificially with a needle on a glass bridge X (25 cm), while 10μL of pure hexane was laid on a controlled bridge C. Both bridges X and the C were maintained during 10 min at 25, 35, 45 or 55°C. Both bridges were then cooled down during 5 min at room temperature (25°C). In order to test whether the ants were able to choose the previously marked bridge, a Y-shaped device was constituted with bridges X and C as the diverging branches, none of them leading to food (see Appendix 7.5.A, Fig. 7.12). The location of both bridges (left or right side of the Y) was randomly chosen at each trial. Ants crossing either branches were counted during 2 min after the connexion of the bridges. Experiments were performed following a factorial procedure with six artificial nests for each species. Five replicates were conducted at each temperature for each nest and extract concentration was randomly attributed so as to obtain 5 replications of each dilution at each temperature for each species.

The probability of choosing bridge X was analysed by fitting a GLM. The dependent variable bound the counts of ants crossing bridge X (success) and C (failure). Predictor variables were the species (categorical variable), the temperature of treatment, and the exudate dilution. As temperature effect continuity was noticed in a previous study (chapter 6), treatment temperature was included as a continuous variable. Since no information were available on the effect of dilution, it was included as a 3-levels categorical variable. A full GLM including all effects and interactions was fitted with the `quasibinomial` family. Non-significant interactions according to an F test on the resulting scaled deviance were progressively removed.

7.2.5 The effect of high temperatures on pheromone decay

"Pheromone" exudates (initial solution) were obtained by the extraction during 24 hours of 150 gasters excised from chilled ants with 1 mL hexane. We aimed to analyse the chemical composition of the pheromone exudate in the same treatment conditions as the behavioural experiment. For this purpose, we developed a technique to retrieve chemical trails laid on a glass bridge that consisted in carefully rinsing the glass with dichloromethane. To control the effectiveness of our technique, we analysed and compared the initial solution (extract) with a retrieved solution (control). A first chromatography (extract) was processed with 20 μL of the initial solution dilluted with 1,4 mL dichloromethane. 20 μL of the initial solution were deposited on a glass slide with a needle. In the case of the control solution, the glass slide was immediately washed with 1,4 mL dicholoromethane, and the solution retrieved was analysed. In the case of temperature treatments, the glass slide was maintained during 10 min at the studied temperature (25, 35, 45 or 55°C), then washed and the retrieved solution was analysed.

Before analytical chromatography, 5 μL of C24 (375.10^{-5} mg) were added as internal standard. Compounds were separated using a gas-chromatograph (GC-2010 *Shimadzu*) with a DB-5HT fused silica capillary column (length 30m, inner diameter 0,25mm, and film thickness 0,10μm). The temperature program started at 50°C during the initial 2 min, raised to 200°C at 10°C.min^{-1}, then raised to 300°C at 20°C.min^{-1}, and held at 300°C for the last 5 min.

Compounds with more than 100 ng in the extract solution were selected. For any of those compounds, the quantity was recorded for all the treatments. The quantity of compounds of the same chemical family were summed. First, a Friedman rank sum test was performed on all the solutions (extract, control, 25, 35, 45 and 55°C) for all family of compounds. If any differences were detected, Kruskal-Wallis rank sum tests were performed on each family of compounds. The same procedure was then repeated for temperature treatment solutions (25, 35, 45 and 55°C).

7.3 Results

7.3.1 The importance of temperature on ant foraging

Once seasonal and daily variations of *T. nigerrimum* and *A. senilis* had been accounted for, the foraging activity of both species covaried significantly with ground temprerature (Table 7.2). However, the effect of temperature was different according to the species and the days. The days that showed similar pattern of variations could be grouped into a "season" (Fig. 7.3). The effect of ground temperature was better taken into account as a third-degree polynomial, estimated at each season, for each species (Table 7.2). For *T. nigerrimum* , ground temperature was not significant for two seasons. Both in spring and late fall, foraging activity variations could be explained by the daily rhythm of this species (Fig. 7.3). However, for the other seasons, ground temperature significantly structured the residuals. In the two summer periods and in early fall, foraging activity was higher than expected by the circadian rhythm at favourable temperatures (between 20 and 35°C) whereas, activity level was lower than expected at high temperatures (Fig. 7.3). For *A. senilis* , all the foraging activity variation could be explained by the circadian rhythm. For this species, the estimation of the temperature polynomial was not significant regardless of the seasons (Fig. 7.3).

Table 7.2 — Analysis of Variance Table of the linear model analysing the residuals of the foraging activity once the different circadian rhythms of the two species *T. nigerrimum* and *A. senilis* was taken into account. The effect of temperature variations is significantly different according to both the season and the species.

Effect	Df	F value	P value
Species	1	2.1	0.144
Season	4	0.8	0.521
Temperature	1	70.5	<0.001
Temperature^2	1	246.1	<0.001
Temperature^3	1	0.6	0.427
Species:Season	4	1.0	0.405
Species:Temperature	1	82.4	<0.001
Season:Temperature	4	8.2	<0.001
Species:Temperature^2	1	86.0	<0.001
Season:Temperature^2	4	9.1	<0.001
Species:Temperature^3	1	12.1	<0.001
Season:Temperature^3	4	2.7	0.031
Species:Season:Temperature	4	3.7	0.006
Species:Season:Temperature^2	4	6.2	<0.001
Species:Season:Temperature^3	4	6.1	<0.001
Residuals	444		

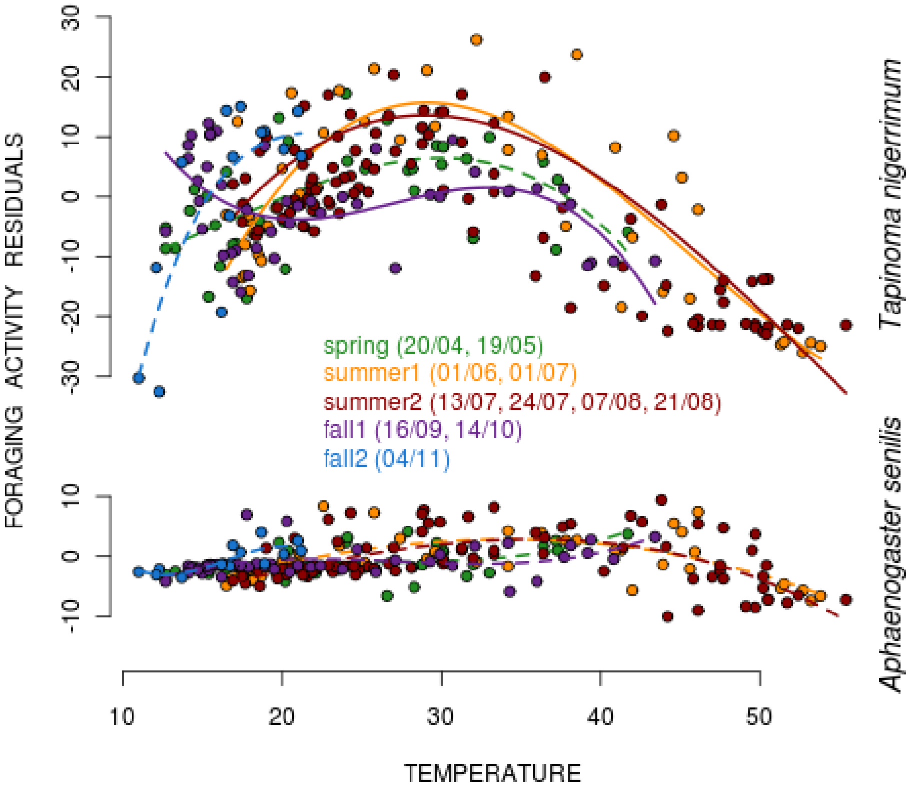


Figure 7.3 — Foraging activity residuals are differently structured by temperature variation according to the species and the season. Residuals of the foraging activity once taken into account the circadian rhythm (points) are superposed with the estimations of the linear model (lines). Dot-dashed lines stand for non-significant temperature effect. Non-significantly different days were grouped into a same level of the factor season differentiated by colours.

7.3.2 Pheromone identification

Tapinoma nigerrimum The chemical profiles of *T. nigerrimum* gasters were qualitatively identical to those of the close species *T. simrothi* with quantitative variations (Fig. 7.4). The gaster extracts contained different compounds. Isomers of the ketone iridodial were the major compound (63.05% ± 8.09), but some light ketones (2-methyl-4-heptanone, sulcatone and 2-nonanone, 29.38% ± 8.27), some isomers of an aldehyde, iridomyrmecin (7.16% ± 4.05), some alkanes (0.31% ± 0.45) and some alcohols (0.11 % ± 0.17) were also present. Some traces of substances such as heptadecane, heptadecene, nonadecane and nonadecene were also detected. The average quantity of each compound per individual was variable due to worker polymorphism. There was about 116.7 ± 19.1 ng of light ketones, 259.7 ± 56.3 ng of iridodials, and 21.5 ± 5.4 ng of iridomyrmecins.

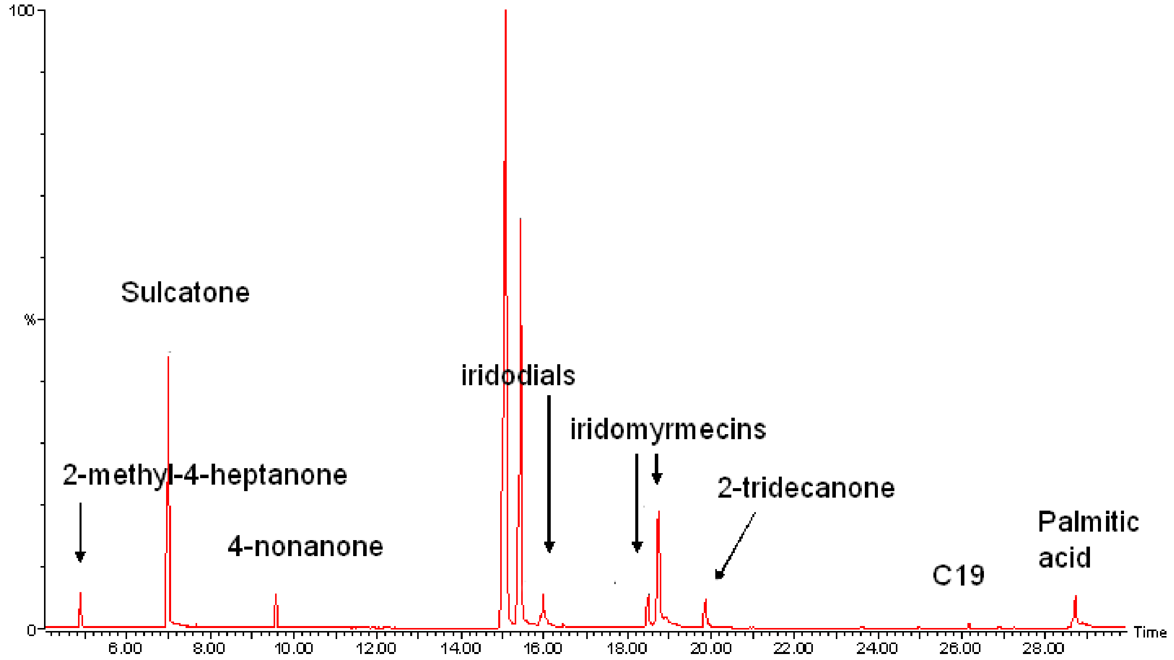


Figure 7.4 — Chromatogram of *T. nigerrimum* gasters extract.

The cuticular hydrocarbon profiles of *T. nigerrimum* were similar to previously published data, but were very different from those of *T. simrothi* (Berville et al., 2010).

We confirmed that the chemistry profile of *A. senilis* was identical to data previously obtained on this species (Lenoir et al., *In prep.*).

7.3.3 The effect of high temperatures on ant behavioural response

At 25°C, significantly more workers of both species chose bridge X rather than bridge C. The choice was more consistent over trials in *T. nigerrimum* than in *A. senilis* (Fig. 7.6). For both species, raising temperature decreased the probability of choosing bridge *X* regardless of the dilution (t=-3.7, -6.5, p<0.001). However, *T. nigerrimum* was more affected by the rise of temperature than *A. senilis* (t=-2.5, p=0.012). Gaster extract dilution was essential to predict the probability of choosing bridge X and its effect was different between the two species (Table 7.5). In *T. nigerrimum* , workers choosiness decreased significantly with pheromone exudate dilution (t=-9.8, -3.8, p<0.001). *A. senilis* was not sensitive to the first dilution (1 vs 1:10, t=1.1, 0.273), but the choice was significantly higher when exposed to a first-diluted than to a second-diluted exudate (1:10 vs 1:100, t=-2.9, 0.004).

Table 7.5 — The choice of an artificially marked bridge in an Y-shaped device depends on the species, the temperature treatment, and the dilution of the gaster extract. Analysis of Deviance Table of the selected GLM (family: quasibinomial, link: logit, Response: Number of ants crossing bridges X and C). Terms were added sequentially (first to last).

Effect	Df	Resid. Df	F-value	P-value
Temperature	1	238	45.2	< 0.001
Species	1	237	272.8	< 0.001
Dilution	2	235	56.0	< 0.001
Species:Dilution	2	233	38.3	< 0.001
Species:Temperature	1	232	6.4	0.012

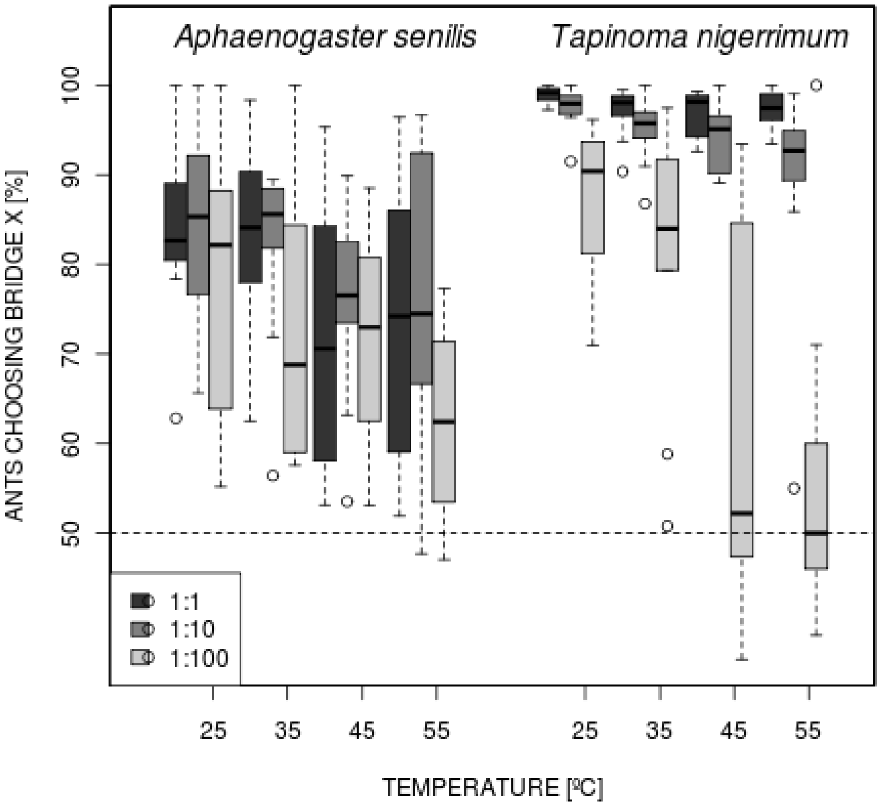


Figure 7.6 — The percentage of ants choosing bridge X differs according to the interplay between pheromone exudate dilution and treatment temperature in the two species *Tapinoma nigerrimum* and *Aphaenogaster senilis*.

7.3.4 The effect of high temperatures on pheromone decay

At the chemical level, *T. nigerrimum* trail pheromone appeared more stable and less sensitive to temperature raising than *A. senilis* pheromone. In *T. nigerrimum* , the chromatographic analysis did not present any differences due to the temperature treatment (Table 7.7). On the contrary, in *A. senilis* , temperature affected significantly the concentration of most compounds (Table 7.9).

In *T. nigerrimum* , 4 groups could be distinguished. The first functional group was composed of extremely volatile ketones that disappeared once the trail had been laid (Fig. 7.8). These light ketones were the 2-Methylheptan-4-one, the sulcatone, and the Nonan-2-one. Both the second and third groups were heavy ketones. They had short life-times since they persisted once laid, but less than 10 min (presence in the control solution and absence in the 25°C treatment, Fig. 7.8). Iridomyrmecins formed the second group. The third group was the tridecan-2-one. The fourth group was composed of very stable aldehydes, the iridodials. Their quantity did not vary between all the solutions (Table 7.7).

In *A. senilis* , we also differentiated 4 groups according to their molecular weight. The first group was tridecane (C13). Its concentration was low (<250 ng per sample), and reduced with temperature treatment (Table 7.9, Fig. 7.10). The second group was composed of pentadecene plus a pyrazine and pentadecane plus anabaseine. It was not possible to differentiate the alkanes from alkaloids as they had the same retention times. Alkanes originate from the Dufour gland while alkaloids originate from the poison gland. Their concentration decreased with time (Fig. 7.10) and was extremely sensitive to temperature treatment (Fig. 7.10). They disappeared completely from 35°C temperature treatment (Fig. 7.10). The third group was formed by three C17 alkanes and alkenes. They showed qualitatively the same pattern as the second group, but their initial quantity was lower, and they totally disappeared from 55°C temperature treatment (Fig. 7.10). The fourth group was stable, and the quantity of its compounds did not change between the different solutions (Table 7.9). It was formed by C19 alkene and C19.

Table 7.7 — *Tapinoma nigerrimum* gaster exudate composition was independent of temperature treatment. Nonparametric tests were performed on the quantity of the compounds established by gas-chromatography.

Discriminating effect	Test	df	χ_2	p-value
ALL SOLUTIONS[1]				
All compounds	Friedman	15	36.9	0.001
Ketones	Kruskal-Wallis	5	14.9	0.011
Iridodials	Kruskal-Wallis	5	7.0	0.220
Iridomyrmecins	Kruskal-Wallis	5	14.9	0.011
Tridecanone	Kruskal-Wallis	5	14.7	0.012
TEMPERATURE TREATMENTS[2]				
All compounds	Friedman	11	11	0.443

[1] identified eventual differences between all the analysed extracts (including solution "Extract" and "Control").

[2] tested differences between solutions according to their temperature treatment (25, 35, 45, or 55°C).

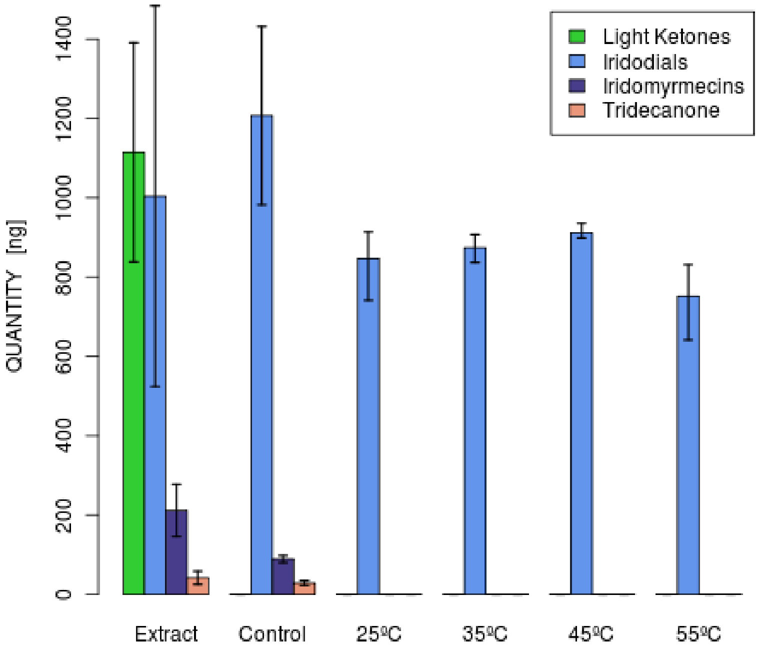


Figure 7.8 — *Tapinoma nigerrimum* gaster exudate composition according to the different treatments. The different solutions were analysed by gas-chromatography on an initial concentration of 3 gasters.

Table 7.9 — *Aphaenogaster senilis* gaster exudate composition was significantly dependent on temperature. Nonparametric tests were performed on the quantity of the compounds established by gas-chromatography.

Discriminating effect	Test	df	χ_2	p-value
ALL SOLUTIONS[1]				
All compounds	Friedman	15	51.2	<0.001
C13	Kruskal-Wallis	5	13.9	0.016
C15/alkaloids	Kruskal-Wallis	5	14.6	0.012
C17	Kruskal-Wallis	5	14.0	0.016
C19	Kruskal-Wallis	5	6.8	0.233
TEMPERATURE TREATMENTS[2]				
All compounds	Friedman	11	35.1	<0.001
C13	Kruskal-Wallis	3	9.5	0.023
C15/alkaloids	Kruskal-Wallis	3	10.7	0.013
C17	Kruskal-Wallis	3	9.6	0.022
C19	Kruskal-Wallis	3	4.1	0.248

[1] identified eventual differences between all the analysed extracts (including solution "Extract" and "Control").

[2] tested differences between solutions according to their temperature treatment (25, 35, 45, or 55°C).

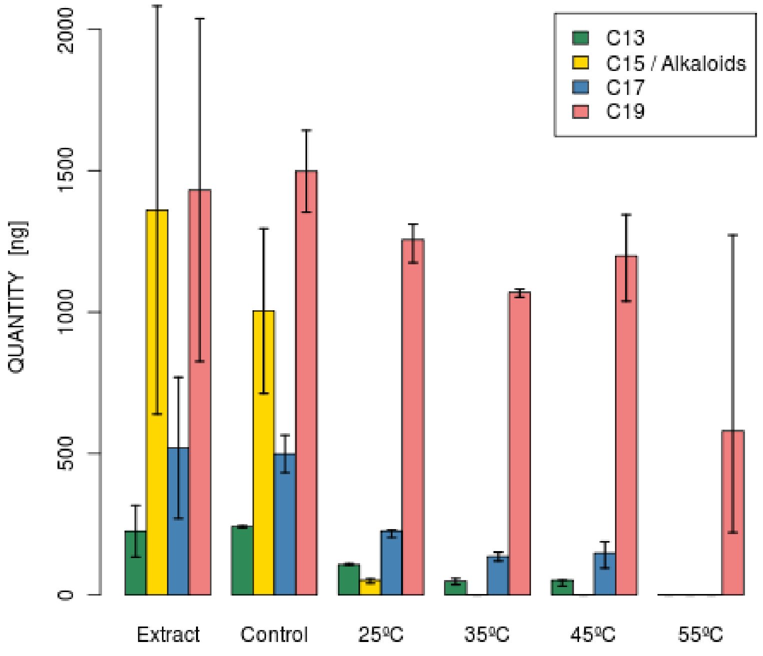


Figure 7.10 — *Aphaenogaster senilis* gaster exudate composition according to the different treatment. The different solutions were analysed by gas-chromatography on an initial concentration of 3 gasters.

7.4 Discussion

High temperature affected differently the foraging behaviour of *Aphaenogaster senilis* and *Tapinoma nigerrimum* . In the field, the activity of *T. nigerrimum* was more dependent on temperature variations than *A. senilis* . The effect of exposing trail pheromone to raising temperature was different at the behavioural and the chemical level. On the one hand, during the trail-following experiment, raising temperature affected *T. nigerrimum* workers choice more than *A. senilis* . On the other, *T. nigerrimum* trail pheromone composition was not changed significantly by heat exposition while *A. senilis* recruitment pheromone was.

Field ecologists studying temperature effect on activity rhythm might always wonder how much of a given pattern is due either to the circannual and circadian rhythmicity or to the temperature. Indeed temperature is highly correlated with both the season and the hour of the day. In this study, we chose to attribute as much variability as possible to the intrinsic rhythms of the species. As expected, the two species showed very different patterns of foraging activity both daily and seasonally (Cros et al., 1997; Cerdá et al., 1997, 1998a). Once these differences were taken into account, we tested whether temperature could explain the remaining variability. Temperature was a good predictor for dominants foraging variability. On the other hand, temperature did not explain more variability than the inner rhythm of subordinates. As suggested by Andersen (1992), the abundance of dominants was limited by temperature variation. Subordinates tend to be more tolerant to high temperatures (Bestelmeyer, 2000; Cerdá et al., 1998a), and their foraging activity is less restricted by environmental fluctuation than by the biotic competition (Wittman et al., 2010).

When focusing on the foraging efficiency, measured as trail-following intensity, high temperatures also appeared more incapacitating for dominants than for subordinates. The pheromone alteration due to temperature was more determinant for ants choice in the mass recruiting species than in the group foraging species. Nevertheless, there was no evidence for pheromone deterioration due to raising temperature for *T. nigerrimum* while there was a significant decay of some chemical compounds of *A. senilis* recruitment pheromone. In short, temperature raising had a heavier effect on the pheromone of *A. senilis* , but a stronger impact on the trail-following behaviour of *T. nigerrimum* . Two reasons might be suggested to explain these results. First, the reduction in trail efficiency due to temperature raising might be less important in *A. senilis* because the trail is not very efficient per se. *A. senilis* was not sensitive to the first dilution, which means that raising pheromone concentration does not necessarily improve trail following in *A. senilis* . Indeed, group foraging species might rely on other kind of cues such as direct interaction with the leader (Hölldobler, 1971). Secondly, the concentration of the pheromone exudate might be determinant in both analyses.

The third dilution at which temperature effect was unequivocal on *T. nigerrimum* workers choice (Fig. 7.6) was far more diluted than the solution that we analysed chemically. There might be an effect of saturation at high concentration, making small differences in pheromone composition undetectable by chromatography analyses.

Mass and group-recruitment illustrated two different investments. In the case of the mass recruitment, there was a high investment in chemical stability but individuals were highly dependent on the efficiency of the pheromone. Indeed, in the composition of *T. nigerrimum* extract, the iridodials were remarkably stable. These compounds also used in the recruitment process of a very close species *Tapinoma simrothi* have a half-life of 11 days (Simon and Hefetz, 1991). Such a great persistence of the pheromone might be advantageous in the exploitation of stable food sources such as aphids-honeydew (Cerdá et al., 1989). Notwithstanding, despite this pheromone stability, ants choice was affected by temperature treatment on the pheromone. To efficiently forage at high temperatures, the trail might thus be constantly reinforced. As a consequence, individuals would be more exposed to high temperatures. The strong limitation of dominant species by high temperature in their foraging schedule might thus rely on the interplay between the metabolic cost on foragers and the decay of the pheromone. Regarding group-recruitment, species bet probably more on individual skills than on chemical efficiency. The trail pheromone was not very stable, and ants presented a huge variability in their behaviour regardless of the temperature treatment (Fig. 7.6). The foraging efficiency of this species might more depend on individual skills such as the load size (Cerdá et al., 1998b) or orientation abilities like in individual foraging species (Collett et al., 1992).

We focused on the reducing effect of high temperatures on trail pheromone efficiency according to the kind of recruitment used. In our model system, group-recruitment pheromone appeared more sensitive to temperature raising than mass-recruitment pheromone at the chemical level. Notwithstanding, at the behavioural level, ants' trail-following was more altered in the mass-recruiting species than in the group-recruiting species. These results illustrate the necessity of bridging the gap between chemical and behavioural ecology in order to get a better understanding of what occurs at the community level, where most of the dominant species are mass-recruiting.

7.5 Appendix

7.5.A Pictures of the experiments

A. senilis

T. nigerrimum

Figure 7.11 — Gaster excision from chilled ants in view of chemical compounds extraction.

Figure 7.12 — Y-shaped device for testing extract detection. The whole device stands in a wood box in order to homogenise light and other environmental factors that could interfere in ants' choice. On the picture, *T. nigerrimum* workers follow the gaster extract artificially laid on the right arm of the Y.

7.5.B Bayesian inference

We adapted the mechanistic model presented in chapter 6 to the behavioural experiment presented in this study. In this experiment, temperature treatment T_e was 25, 35, 45, or 55°C; dilution treatment C_e was 1, 0.1, or 0.01; and the time of exposition t_h was 10 min.

In this case, the stochastic links were:

$$\begin{aligned} C_j &= C_e \, e^{-\beta t_h \sqrt{T_e + T_{ref}}} \\ \mathbb{P}_j &= \frac{(k + C_j)^n}{(k + C_j)^n \; + \; k^n} \end{aligned} \tag{7.1}$$

Data were then related to the model output assuming a binomial error model:

$$X_j \sim \mathcal{B}in(\mathbb{P}_j, Tot_j)$$

As priors, we chose large non-informative distributions: $\beta \sim \mathcal{G}amma(shape = 0.001, rate = 0.001)$, and $k \sim \mathcal{G}amma(shape = 0.001, rate = 0.001)$. Other parameters were fixed: $T_{ref} = -24$ and $k = 2$. Bayesian inference was performed using Markov Chains Monte Carlo (MCMC) algorithms with the *rjags* R package (Plummer, 2009) (Implementation code available upon request).

Our estimates differ between the two species (Table 7.13). On the one hand, *T. nigerrimum* pheromone is more sensitive to high temperatures than *A. senilis* (higher β estimate). On the other hand, *A. senilis* display a higher degree of attraction to an unmarked branch than *T. nigerrimum* (higher k estimate). This estimation illustrates that the foraging activity of *A. senilis* is not as pheromone-dependent as *T. nigerrimum* .

Table 7.13 — Bayesian parameter estimates for *T. nigerrimum* and *A. senilis* (95% credible intervals). β represents the effect of high temperature (>25°C) on pheromone decay, and k stands for the attractiveness of an unmarked branch. Other parameters were fixed: $T_{ref} = -24$ and $k = 2$

SPECIES	β			k		
	2.5%	50%	97.5%	2.5%	50%	97.5%
T. nigerrimum	0.050	0.0563	0.063	0.003	0.004	0.005
A. senilis	<0.001	<0.001	0.009	0.723	0.969	1.138

Regarding the effect of temperature on *T. nigerrimum* , the estimate was consistent with the parameter values estimated in the chapter 6 ($\beta = 0.056$ [0.051; 0.062]). This similarity supports the pertinence of our mechanistic model. However, in chapter 6, fixing $n = 2$, parameter k estimate was closed to 39.59. This huge dissimilarity might be explained by differences in the experimental protocols. In the experiment presented in chapter 6, the effect of time was also measured: experimental colonies were connected to the Y-shaped device at t=0, and ants crossing both marked and unmarked branches were counted until t=30. Even if ants had first chosen the marked branch, they had time to explore the unmarked branch. In the experiment presented here, ants are counted only 2 min. Only the first choice is therefore taken into account. The degree of attraction of the unmarked branch estimated in chapter 6 might thus be overestimated.

7.5.C Chemical profiles of gaster extracts according to temperature treatment

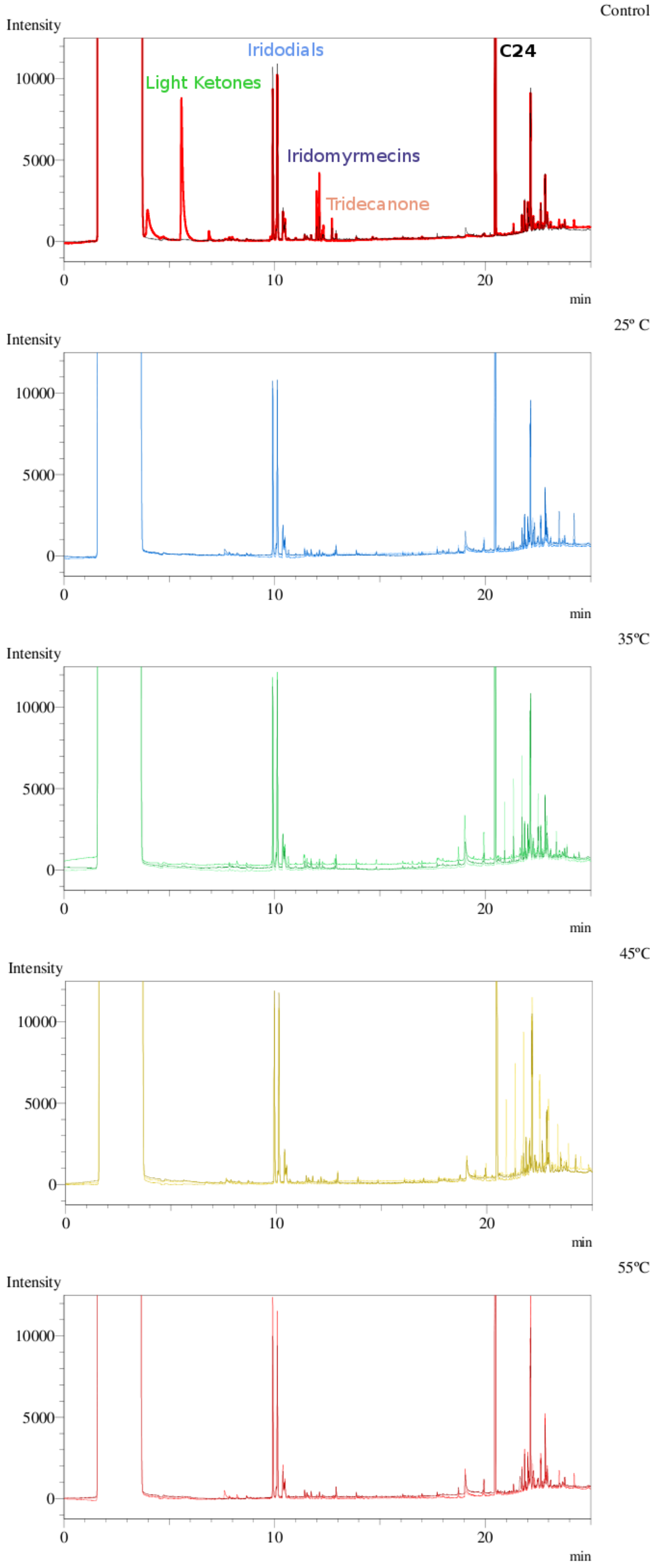


Figure 7.14 — Chromatograms of *T. nigerrimum* gaster extracts according to temperature treatment. The top graph represents the controls and superposes the initial solution ("extract", in thick red lines) with the retrieved solution ("control", in thin black lines).

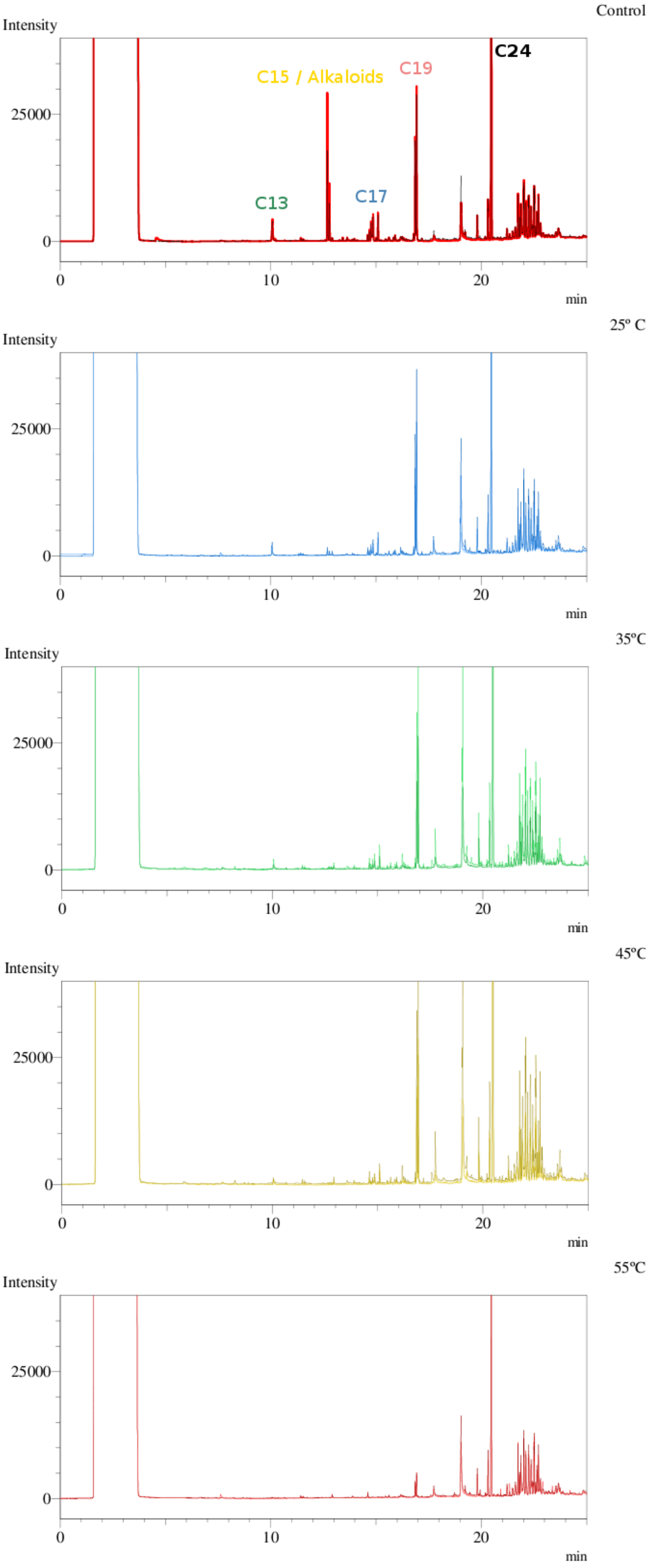


Figure 7.15 — Chromatograms of *A. senilis* gaster extracts according to temperature treatment. The top graph represents the controls and superposes the initial solution ("extract", in thick red lines) with the retrieved solution ("control", in thin black lines).

CHAPTER 8

To forage or not to forage, the question of high temperatures [1]

In many organisms, interspecific interactions integrate both biotic and abiotic factors. In Mediterranean environments submitted to extreme and variable temperatures, ant communities are structured by the interplay between thermal tolerance to high temperatures and competition. In this paper, we compared the foraging behaviour between dominant and subordinate species both under controlled conditions and in the field. On the one hand, we tested whether the choice of ants to face dangerous temperatures was species and state-dependent (according to the energetic reserve of the colony and the presence of brood). On the other hand, we determined if this foraging decision was dependent on the time exposed to dangerous temperatures. Unexpectedly, our results showed that the subordinate species was choosier about temperatures than the dominant species. The state-dependency decision was similar between the two species, and consistent between preferred and critical temperatures. However, when varying the foraging distance, a very different pattern appeared: the subordinate species was much bolder than the dominant regarding the duration of exposition to dangerous temperatures.

8.1 Introduction

Competition is a cornerstone of ant community structure (Hölldobler and Wilson, 1990; Andersen, 1992; Parr et al., 2005). Ants compete in transitive dominance hierarchies where behaviourally dominant species successfully dislodge behaviourally subordinate species (Fellers, 1987; Savolainen and Vepsäläinen, 1988; Perfecto, 1994; Sanders and Gordon, 2003).

---

[1] Co-authors: **R. Boulay, C. Bernstein, X. Cerdá**

An interesting challenge in ant communities is thus to understand what promotes the coexistence between dominant and subordinate species (Andersen, 2008). There are numerous evidences of coexistence being facilitated by niche partitioning (Savolainen and Vepsäläinen, 1989; Albrecht and Gotelli, 2001). For instance, species often differ in the size (Cerdá et al., 1998b; Lebrun, 2005) and the kind (Sanders and Gordon, 2003; Blüthgen and Fiedler, 2004) of resource they consume. Different interspecific trade-offs are also known to prevent competitive exclusion. The most documented trade-off underpinning local species coexistence is the discovery-dominance trade-off (Fellers, 1987; Savolainen and Vepsäläinen, 1988; Perfecto, 1994; Davidson, 1998; Holway, 1999; Adler et al., 2007; Lebrun and Feener, 2007). A negative correlation between resource discovery and dominance abilities is a common feature in many ant communities: the first species in discovering resources are behaviourally subordinate. The second trade-off with a key role in structuring ant communities is the dominance-thermal tolerance trade-off (Cerdá et al., 1998c,a; Bestelmeyer, 2000; Lessard et al., 2009; Wittman et al., 2010). Behaviourally subordinate species are more tolerant to stressful temperatures than dominants. Species differ in their thermal preferences, and thereby forage at different periods according to temperature fluctuation (Cros et al., 1997; Bestelmeyer, 1997; Retana and Cerdá, 2000). In Mediterranean-like communities, the wide range of temperature variations distinguishes different "thermal niches" allowing the coexistence of species with different foraging behaviour regarding temperatures (Cerdá et al., 1998a).

Social insects do not maximise the net energetic gain but the colony growth and reproduction, which involves trade-offs between energy return to the colony and worker mortality (Houston et al., 1988b; Wolf and Schimd-Hemped, 1990; Nonacs, 1990; Nonacs and Dill, 1990, 1991; Nonacs and Calabi, 1992). Many factors might increase foragers mortality. First of all, biotic interactions within the same trophic level such as intra and inter specific competition (Hölldobler and Wilson, 1990; Nonacs and Dill, 1991) represent a danger by increasing mortality and trigger an altered behavioural response (Nonacs and Calabi, 1992). Secondly, biotic interaction that concern higher trophic levels such as predation (Whitford and Bryant, 1979) and parasitism (Feener, 2000) increase forager mortality and provoke a reduction in the number of foragers (LeBrun and Feener Jr, 2002). And last, but not least, the rigor of habitat such as extreme temperatures are a source of danger (Lighton and Turner, 2004; Maysov and Kipyatkov, 2009). In ants, temperature regulates the foraging activity both daily and seasonally (Marsh, 1985; Pol and Lopez de Casenave, 2004; Bucy and Breed, 2006; Azcárate et al., 2007; Chong and Lee, 2009). In Mediterranean communities, high temperatures might be critical for ants survival, and Cerdá et al. (1998a) showed that two different behavioural strategies protect against this danger: Dominant species that are generally heat-intolerant have a "minithermy" strategy by avoiding exposition to high temperatures even if they could eventually tolerate them, while subordinate species that tend to be more heat-tolerant have a "maxithermy" strategy and forage at high temperatures even close to their critical thermal maximum.

From an adaptive perspective, an organism should respond to its internal state and to its environment (Houston et al., 1993). State-dependent theory predicts the optimality of plasticity as the response of the organism to its state (McNamara and Houston, 1996). In ants, the collective response is adjusted to the starvation level of the colony (Hangartner, 1969; Mailleux et al., 2006). However, the energetic state of the colony depends mostly on the number and the development stage of larvae that define the colony nutritional needs (Portha et al., 2002, 2004). Both starvation level and brood presence, as essential components of the internal state of the colony, might therefore be influencial factors in the colony foraging decision.

This study focused on the foraging behaviour dependence to high temperature of dominant and subordinate species. To get a better understanding on the foraging decisions regarding temperature and behavioural dominance status, we addressed the following questions: i/ Are subordinates more inclined to forage at a temperature that might be dangerous for individuals than dominants ? ii/ Is this decision state-dependent (ie depending on the energetical reserve and on the abundance of brood)? Is this state-dependency different between species ? iii/ Does this foraging choice depend on the expected time of exposition to high temperature? Does foraging distance of subordinate and dominant species depend similarly on temperature?

8.2 Materials and methods

8.2.1 Model species and study site

To test behavioural differences between dominant and subordinate species under controlled conditions, we worked with *Tapinoma nigerrimum* (Fig. 6.1) as dominant and *Aphaenogaster senilis* (Fig. 7.1) as subordinate. In Mediterranean communities, *T. nigerrimum* and *A. senilis* state respectively in the upper and lower sites of the dominance hierarchy (Cerdá et al., 1997). *T. nigerrimum* is a mass recruitment species, more aggressive and able to dominate a larger proportion of baits than *A. senilis* (Cerdá et al., 1997). *T. nigerrimum* have polygynous and polydomous colonies with many thousands of small polymorphic workers (Cerdá et al., 1989; López et al., 1997; Gomez and Espadaler, 1998). Colonies of *A. senilis* are monogynous and monodomous with 200 to 3,000 workers (Boulay et al., 2007b; Cerdá et al., 2009). *T.*

nigerrimum is a heat-intolerant species. Its Maximal Activity Temperature (MAT) is 24°C and its Critical Thermal Limit is 42°C. *A. senilis* is a thermophilic species, with a MAT of 42°C and a CTM of 46°C (Cerdá et al., 1998a).

Colonies were freshly collected in the field in Andalucia (South of Spain). For each species, 20 experimental units (or nests) were constituted so as to obtain comparable numbers of workers (between 800 and 1500). Experimental nests were installed in plastic boxes with a plaster bottom. Humidity was maintained by regular moistening the plaster and with small glass tubes with water and a cotton plug. Surrounding temperature remained at 25°C (± 1°C) and humidity at about 35%. In all nests, queens were removed. Experiments aimed to estimate the effect of the presence of brood and/or starvation on foraging decisions. For both species, the brood was removed from half of the nests one week before the first trial of the colony. Fed nests received at least two dead maggots the night previous to the test, and starved nests did not received any food for seven days.

The field experiment was conducted in Doñana National Park (South of Spain), in July 2009. The study area was an open shrubland (see Appendix 8.5.A, Fig.donana5). Seven ants species were found at baits during this sampling: *Lasius grandis* (56%), *Aphaenogaster senilis* (21%), *Cataglyphis floricola* (11%), *Plagiolepis spp.* (6%), *Crematogaster sordidula* (2%), *Tapinoma nigerrimum* (2%), *Tetramorium inpurum* (2%), and *Messor spp.* (1%). Only the two most abundant species were considered in this study: *A. senilis* and *L. grandis* .

Figure 8.1 — *Lasius grandis* worker (photo: F. Amor).

Lasius grandis (Fig. 8.1) is known as a native dominant species in other Mediterranean communities (Gómez et al., 2003; Wetterer et al., 2006; Wetterer, 2006). Previously to the field study, we studied the thermal preferences of this ant species because of absence of data on this topic. We aimed to compare if it was equivalent to the other dominant *T. nigerrimum*. Activity at baits was measured in May in Las Beles shrubland (Doñana National Park). Bait occupation was evaluated using 48 baits distributed in two transects with six groups of four different baits (plastic discs with cheese, ham, biscuit or diluted honey) that could not be transported to the nest by individual workers. Distance between baits within group was 1m, between groups 5m, and between transects was 50m. Baits were installed at 07:00 am. Activity on baits was measured each hour from 08:10 to 23:30. From our results (Fig. 8.2), we concluded that both species, *T. nigerrimum* and *L. grandis* have a similar activity pattern in Doñana, with a very close value of MAT (24°C for *T. nigerrimum* , 22°C for *L. grandis*) as it occurs with most dominant ant species (Cerdá et al., 1997).

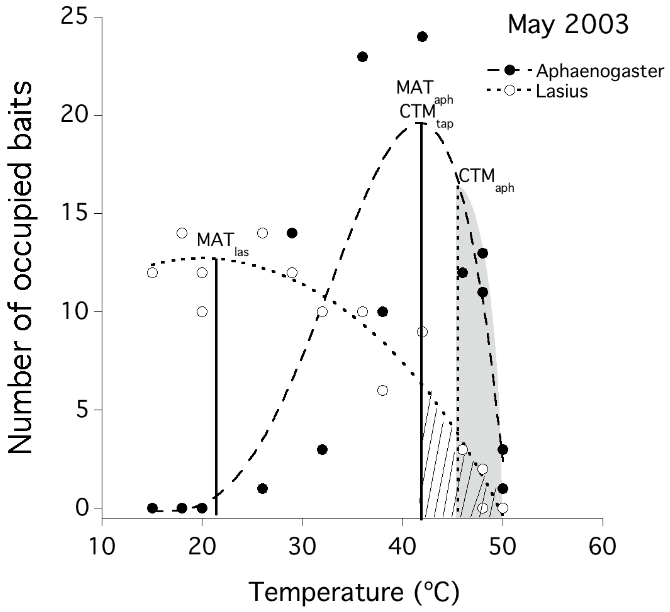


Figure 8.2 — Number of baits occupied by *Aphaenogaster senilis* and *Lasius grandis* according to ground temperature in May (Las Beles, Doñana National Park). Activity curves were fitted with a 4-degree polynomial for *T. nigerrimum* and a 2nd-degree polynomial for *L. grandis*. For comparison, Maximum Activity Temperature (MAT) and Critical Thermal Maximum (CTM) of *A. senilis* and *T. nigerrimum* are indicated. Shaded and striped areas represent activity at stressful temperatures for *A. senilis* and *L. grandis* (assuming a similar thermal tolerance for *T. nigerrimum* and *L. grandis*).

8.2.2 To go out or not to go out at high temperatures?

In the laboratory, the experiment consisted in connecting the nest to an electronic plactronic Selecta hot plate. Ants had to cross the plate to reach the food (40 cm). The food was an artificial diet composed by agar, honey, eggs and vitamins. The hot plate was either at the MAT or at the CTM of the species. All the nests (10 with brood and 10 broodless for each studied species) were tested at both temperatures for each feeding status with a factorial procedure.

We measured the time it took to discover the food source, i.e. the time between the connection of the nest to the hot plate and the moment at which the first ant starts feeding on the bait. Starting from the moment of discovery, a photograph of the food was taken at t = 5, 10 , 15, and 20 min. Ants feeding at bait were counted from these photographs (see Appendix 8.5.A, Fig. 8.9). We also recorded, for some individuals, the duration of their returning trip to the nest.

The first measure we studied was the discovery rate. First and foremost, we evaluated whether there was any variation in the running speed of individuals. Travel time back to the nest was measured for 91 ants (n=31 for *A. senilis* and n=60 for *T. nigerrimum*). We tested the effect of the species, the temperature (as a two-level factor), the presence of brood and the feeding status on this variable. A linear model (on the log-transformed response variable) was fitted using a backward-stepwise procedure. To correct the discovery rate for running speed variations, we defined the hesitation rate $\mathcal{H}$ as the logarithm of the ratio between the time taken to discover the food source and the time taken by the trip back to the nest ($\mathcal{H} = log(\text{Discovery time}) - log(\text{Travel time})$). We calculated the hesitation rate of all replicates using travel time estimations. This quantity was the response variable of a mixed effects model including the nest as a random effect, and species, temperature, presence of brood and fed status as fixed effects. A full model that contained all variables and interactions was built with the `lme` function (R-package `nlme`) and log-likelihood maximisation method. Non significant effects according to a Likelihood-Ratio test were progressively removed.

The second criterion we analysed was the activity level. The maximum activity level (MAL) of each nest was defined as the maximum of the total number of ants feeding at bait during the whole test (summed for t=5, 10, 15, and 20 min). The activity level for a given nest at a given time was the ratio between the effective number of ants feeding at bait at this given time, and the MAL of the nest. This proportion was the response variable of a linear model. The effects of the species (categorical), the feeding status (categorical), the presence of brood (categorical), the temperature of the hot-plate (categorical), and the time elapsed since discovery event (continuous) were studied. A full model including all effects and interactions was fitted, and non-significant interactions were progressively removed. All the analyses were performed using software R (R Development Core Team, 2010) and a 5% level of significance.

8.2.3 How far to forage at high temperatures?

Field work was conducted during four consecutive summer days. Three samplings were conducted each day: in the morning (7 : 50-11 : 00), at midday (11 : 50-15 : 00) and in the evening (18 : 50-22 : 00). Ground temperatures in the transects varied from 14°C to 46°C in the morning (23°C ± 6.0°C), from 26°C to 77°C at midday (50°C ± 11.7°C), and from 22°C to 55°C in the evening (31°C ± 5.7°C).

During each sampling, a hundred baits were placed in five linear series of twenty, with 1 m spacing between baits and between series. Baits were plastic spoons with large-food rewards (cat food and biscuits) that were attractive to ants and could not be transported to the nest in one piece by foragers. Every 2 hours, the species feeding at baits were recorded, as well as the ground temperature near the baits (IR-Thermometer *Extech*). Ants at baits were followed in order to determine nest place, and distances between nests and baits were measured.

The dependent variable was the distance (in meters) between the exploited bait and the nest. The explanatory variables were the temperature of the bait (continuous), the species (categorical), and the interaction between variables. The data were analysed with a Generalized Linear Model (GLM) with a gamma distribution and an inverse link function. Effect significances were tested with an F-test on the scaled deviances.

8.3 Results

8.3.1 To go out or not to go out at high temperatures?

At their respective MAT, *A. senilis* workers ran significantly faster than *T. nigerrimum* workers (t = 2.8, p = 0.007). Conversely, at their respective CTM, *A. senilis* ran significantly slower than *T. nigerrimum* (t = -3.0, p = 0.004). *T. nigerrimum* significantly reduced the duration of their returning trip to the nest at its CTM (t = -6.1, p < 0.001), whereas *A. senilis* travel time was not affected by temperature (t = -0.6, p = 0.542). For both species, neither feeding status nor brood presence affected the running speed of individuals.

A. senilis was better at discovery than *T. nigerrimum* . Even taking into account the running speed differences, *A. senilis* hesitated less than *T. nigerrimum* (t = -3.9, p < 0.001). For the two species, both the presence of brood and the feeding status were significant in predicting

Table 8.3 — The hesitation to forage at high temperatures depends on the species and the state of the colony (presence of brood and starvation). The hesitation rate $\mathcal{H}$ relies on the difference between the time to discover the bait, and the time to travel back to the nest. The effect of brood and feeding status were analysed by a Mixed Effect Model. Analysis of Variance Table of the minimal appropriate Linear Mixed Effect model.

Effect	Num Df	Den Df	F-value	P-value
Brood	1	37	9.91	0.003
Food	1	119	6.86	0.010
Species	1	37	15.18	<.001

the hesitation rate (Table 8.3). Colonies with brood hesitated less than broodless colonies (t = -3.1, p = 0.003). Counterintuitively, fed colonies hesitated less than starved colonies (t = -2.6, p = 0.010). The hesitation rate did not depend on temperature (Table 8.3).

Tapinoma nigerrimum had more ants feeding at bait than *Aphaenogaster senilis* (from 1 to 333 ants for *T. nigerrimum* and from 0 to 134 for *A. senilis*). The analysis of the activity level focused on the different patterns between species. The two species displayed different foraging behaviour according to the temperature, the feeding status, and the presence of brood (Table 8.4, Fig. 8.5, Fig. 8.6). *A. senilis* and *T. nigerrimum* differed both in the intensity

Table 8.4 — The dynamics of the activity level differs according to the species and the state of the colony (presence of brood and starvation). The activity level corresponds to the number of ants feeding at bait corrected by the efficiency of the nest. The effect of brood and feeding status were analysed by a linear model. Confidence intervals of the selected linear model predicting the activity level. The estimation of the different level of the categorical variables were obtained by contrasts modifications.

			SHORT TERM ACTIVITY LEVEL				TIME EFFECT	
SPECIES	STATE		CTM		MAT		CTM & MAT	
	Brood	Food	2.5%	97.5%	2.5%	97.5%	2.5%	97.5%
A. senilis	no	no	0.1148	0.1782	0.2145	0.2778	-0.0067	-0.0027
T. nigerrimum	no	no	0.0868	0.1509	0.1585	0.2212	-0.0032	0.0008
A. senilis	no	yes	0.1006	0.1639	0.1690	0.2323	-0.0067	-0.0027
T. nigerrimum	no	yes	0.0728	0.1364	0.1127	0.1759	-0.0032	0.0008
A. senilis	yes	no	0.1569	0.2202	0.2829	0.3462	-0.0097	-0.0057
T. nigerrimum	yes	no	0.1690	0.2324	0.2664	0.3296	-0.0061	-0.0021
A. senilis	yes	yes	0.1426	0.2060	0.2374	0.3006	-0.0097	-0.0057
T. nigerrimum	yes	yes	0.1548	0.2181	0.2208	0.2841	-0.0061	-0.0021

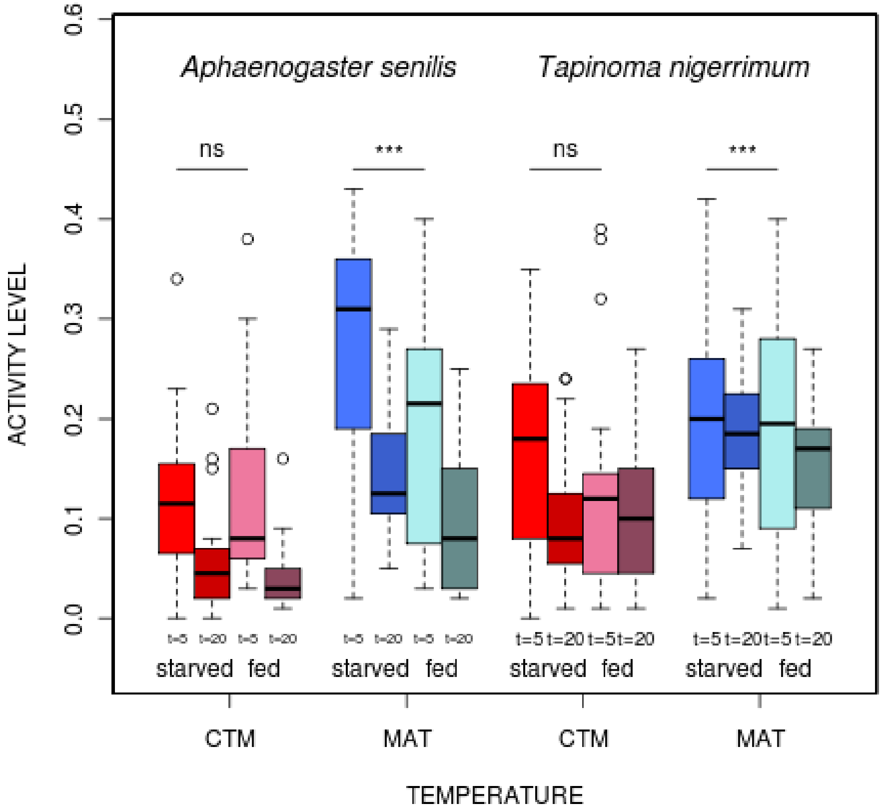


Figure 8.5 — The activity level (number of ants feeding at bait corrected by the maximal efficiency of the nest) is represented as a function of the time elapsed since bait discovery (t=5 and t=20) for each species (*A. senilis* and *T. nigerrimum*), feeding status (starved / fed) and hot-plate temperature (specific CTM / MAT). Significance of the estimation of the linear model (according to the F-test) are indicated above the boxplot (*** = $p < 0.001$, ** = $p < 0.01$, * = $p < 0.05$, . = $p < 0.1$, ns = $p > 0.1$).

(activity level) and the dynamics (time effect) of recruitment. Both species reduced their initial intensity at their Critical Thermal Limit ($t \in [-3.0, -9.6]$, $p < 0.01$). However, quantitatively, *A. senilis* was more sensible to critical temperature than *T. nigerrimum* (t=-2.2, p=0.030). In both species, starved colonies increased significantly their activity level at their MAT (t=4.9, $p < 0.001$), but did not show any differences at their CTM (8.5). The effect of the time elapsed since resource discovery made a distinction between the short term response (intercept) and the long term response (slope). Regarding the presence of brood, both species showed the same sensibility in their short term activity level, but differed in the long term response. In the short term, colonies with brood had more ants feeding at baits than broodless colonies (Table 8.4, Fig. 8.6). *A. senilis* reduced significantly its long term activity level regardless of

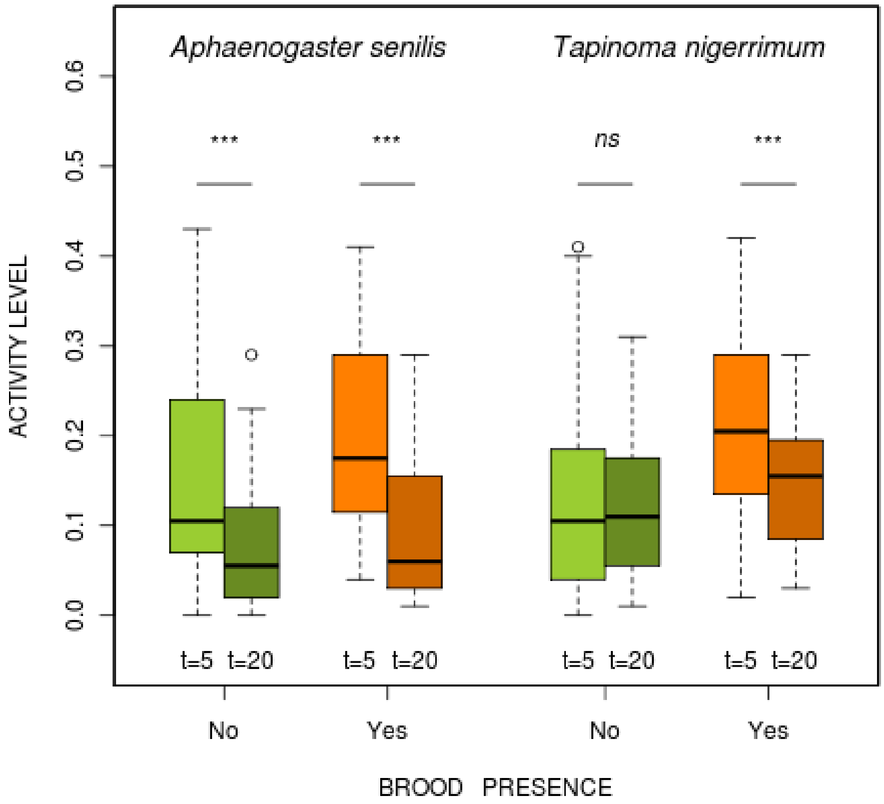


Figure 8.6 — The activity level (number of ants feeding at bait corrected by the maximal efficiency of the nest) according the species, the presence of brood, and the time elapsed since bait discovery. F-test significance indicated above the boxplot (*** = $p < 0.001$, ** = $p < 0.01$, * = $p < 0.05$, . = $p < 0.1$, ns = $p > 0.1$).

the presence of brood (t=-4.7, -7.6, p<0.001). In *T. nigerrimum* , colonies with brood reduced their activity level on the long term (t=-4.1, p<0.001) whereas broodless colonies did not show any difference in their long term activity level (t=-1.1, p=0.25).

8.3.2 How far to forage at high temperatures?

The two most abundant species displayed very different foraging behaviours. First, *Lasius grandis* and *Aphaenogaster senilis* differed in the range of temperatures at which they foraged. *L. grandis* tended to forage at cooler temperatures than *A. senilis* (27°C ± 5.8°C for *L. grandis* and $31^o \pm 7.2^o$ for *A. senilis*). Secondly, they did not forage at the same distance. The distances between baits and nest entrance were shorter in *L. grandis* than in *A. senilis* (Fig. 8.8). When active, *L. grandis* foraged close to the nest (between 0.16 and 2.5 m) whereas *A. senilis* covered large distance to exploit the baits (between 0.5 and 7.4 m). Third, the effect of temperature on the foraging distance was significantly different for the two species (Table 8.7). *L. grandis* foraged significantly closer to the nest when temperature increased (t = - 2.1, p-value = 0.039). Conversely, the effect of raising temperatures on *A. senilis* foraging distance was significantly positive (t = 3.6, p < 0.001).

Table 8.7 — The influence of ground temperature on foraging distance is significantly different on *Lasius grandis* and *Aphaenogaster senilis*. Analysis of Deviance Table of the selected GLM (model: gamma, link: inverse, Response: distance). Terms were added sequentially (first to last).

Effect	Df	Resid. Df	F	P-value
Species	1	703	851.8	<0.001
Temperature	1	702	7.3	0.007
Species:Temperature	1	701	9.6	0.002

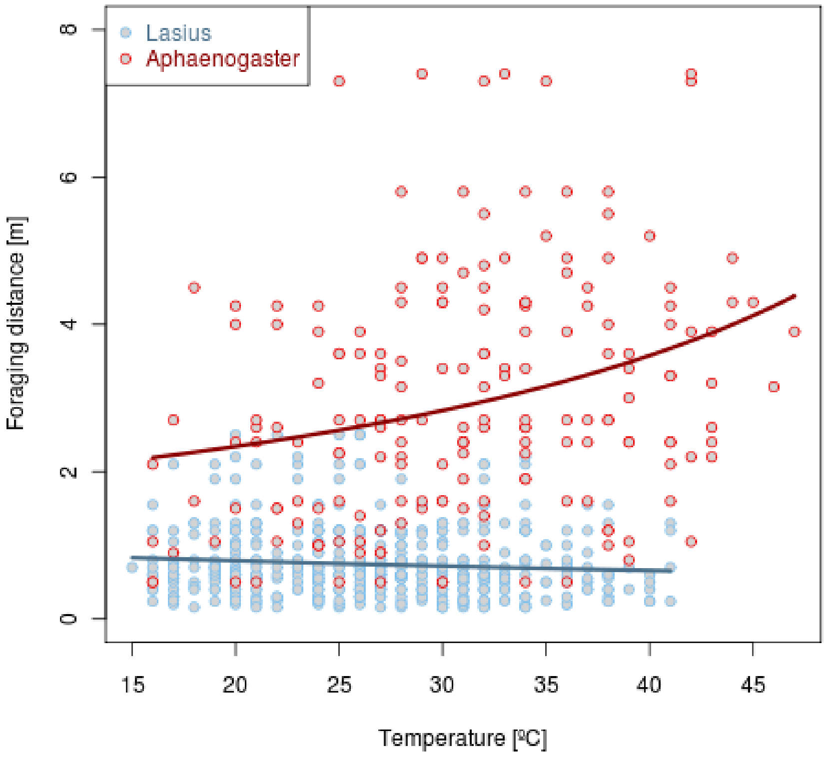


Figure 8.8 — The effect of ground temperature (measured at bait) on the distance between bait and nest entrance differs with species. Field data (points) and model predictions (lines) of the foraging distance are represented for the dominant, *L. grandis* (blue), and the subordinate species *A. senilis* (red).

8.4 Discussion

The present study supplies some responses to our different questions: i/ Both the subordinate *Aphaenogaster senilis* and the dominant *Tapinoma nigerrimum* reduced their activity when temperature raised from their MAT to their CTM. In this experiment, *A. senilis* was more sensitive to the difference of temperature than *T. nigerrimum* . ii/ Starved colonies produced a larger foraging effort than fed colonies, but the difference was equivalent between temperatures and species. Broodless colonies displayed a lower activity level than colonies with brood independently of the temperature and the species. However, *A. senilis* reduced activity over time regardless of the presence of brood while broodless colonies of *T. nigerrimum* had a constant activity level during the 20 min tested. iii/ Dominants reduced while subordinates raised their expected exposition time (foraging distance) when temperatures increased.

In the first foraging decision regarding nest outing, the subordinate species reduced its activity level more than the dominant species. This result runs counter to previous studies. Indeed, Cerdá et al. (1998a) established that subordinate species tend to assume more risk regarding high temperatures than dominants. In particular, regarding our two model species in the field, *T. nigerrimum* performs less than 5% of its foraging activity at "risk condition" whereas *A. senilis* accomplishes more than 15% of its foraging activity at "risk". How can we explain our controversial result? We tested the behaviour of the two species at their respective Maximal Activity Temperature and Critical Thermal Maximum according to the values established by Cerdá et al. (1998a). There could be a margin of error on these values. On the one hand, more than ten years have passed since their statement, and they have been measured on different populations. On the other hand, Cerdá et al. (1998a) did not measure the relative humidity while recording the CTM and the interplay between humidity and temperature might be determinant in ants survival. Notwithstanding, regardless of the exact values of the MAT and the CTM, *A. senilis* responded more to a 4°C temperature raise than *T. nigerrimum* to a 18°C rise. This outcome is rather unexpected. Two explanations might be put forward: i/ The artificial food we used for the experiment contained mostly honey that could be much more attractive for *T. nigerrimum* than for *A. senilis* (Cerdá et al., 1988, 1989). Like kids who would quarrel for chocolate cake but not for celery, it might not be worse facing dangerous temperatures for *A. senilis* , contrary to *T. nigerrimum* . ii/ Our hot-plate was 50cm long. The total foraging time including crossing the hot-plate and feeding was short (<4min). The exposure time to the CTM might not have been long enough to be considered as dangerous. The influence of exposure time can be reached by modifying the distance between nests and baits. However, it was impossible to carry out in the laboratory. The interplay between high temperatures and exposure time had thus been examined in the field. The results showed an opposed foraging behaviour of dominant and subordinate species regarding the exposition time to high temperature. Dominants reduced whereas subordinates increased their foraging time while temperature raised. This outcome supports the idea proposed by Cerdá et al. (1998a) regarding thermal strategies of dominants as "risk-averse" and subordinates as "risk-prone" in Mediterranean ecosystems. However, the terminology of "risk" seems inappropriate to the stress generated by high temperatures. In their definition, Stephens and Krebs (1986) refer to "risk" as a probabilistic variation. In the case of thermal stress, ants do not have the choice between situations defined by randomly distributed variables with equivalent means and different variances (Stephens and Krebs, 1986; McNamara and Houston, 1992; Kacelnik and Bateson, 1996). They have to choose whether or not to face a situation where the probability of death is more or less important. In this case, as for the stress associated to predation (Nonacs and Dill, 1990, 1991), the notion of danger might be less confusing (Stephens and Krebs, 1986).

The subordinate species, when released from competitive interactions with dominants in the laboratory, appeared to be highly sensitive to temperature raising. Nevertheless, when studied in natural conditions, this species increased its foraging distance, i.e. its exposition time while temperature raised. This suggests that for subordinates, the stress generated by high temperatures might be less important than the stress emanating from the presence of the dominants at baits. Competitive interactions are known to affect diet choice (Sanders and Gordon, 2003). Our study indicates that competition might affect temperature preferences. In this case, heat-tolerance of subordinate ant species might be a coevolutive process underpinned by competitive interactions with dominant species, rather than an independent physiological specialization (Dunson and Travis, 1991).

Many of the striking differences between dominant and subordinate species might be explained by the specific biology of the model species. The notable difference in the foraging behaviour of the two species is the mean distance between baits and nests. The dominant species foraged significantly closer to the nest entrance. This phenomenon might be explained by the kind of nest made by the dominant species. Colonies of *Lasius grandis* are polydomous, and the different nest entrances are connected by underground galleries. As the field experiment was conducted in July, environmental conditions were not optimal for workers of the dominant species to forage. They had a low level of activity comparing to the activity showed in spring and only foraged close to the nest. Moreover, the nests often stood in the vegetation, and the baits closest to nest entrance were generally at cooler temperatures. The second main difference between the two model species concerns the foraging strategies. In Mediterranean ecosystems, dominants are often species using mass-recruitment while subordinates forage with more individual strategies. This difference in strategies might explain the use of so different patterns regarding foraging distances. On the one hand, individual foraging species might run on the vegetation and use grassland as a thermal refuge when the sand is too hot (pers. obs.), whereas mass-recruiting species are dependent on the ground substrate to efficiently lay and detect pheromone (Detrain et al., 2001; Jeanson et al., 2003) and cannot use the vegetation trick. On the other hand, the trail pheromone used by mass-recruiting species might decay faster while raising temperature (chapters 6&7) and hot substrate would thereby alter communication between nestmates. The third difference clarifies the difference of behaviour regarding the presence of brood in *Tapinoma nigerrimum* . Indeed, *T. nigerrimum* workers feed larvae by trophallaxis like other *Tapinoma* sp. (Lenoir, 1979). In colonies with brood, foragers might take the time to transmit the food to the nurses or directly to the larvae. In *A. senilis* , workers do not use trophallaxis (Lenoir et al., 2001). The decrease in foraging intensity is more likely due to a disinterest in the kind of food we provided in the experiment.

This study illustrates the integrative role of laboratory and field experiments. Indeed, the zoom we made on behavioural differences between two species in the lab might not reflect the overall complexity of the foraging decisions. Under controlled conditions, the subordinate species appeared more intolerant to stressful temperatures than the dominant. In the field, the opposite pattern was observed. Contrary to the dominant species, the subordinate increased its foraging distance when temperatures rose. These differences underline the lack of essential factors in our experimental setting such as adapted foraging distances, food characteristics, complementary abiotic factors such as the relative humidity and the atmospheric pressure, and last but not least, competitive interactions.

8.5 Appendix

8.5.A Pictures of the experiments

Figure 8.9 — During the experiment, photographs of the bait were taken at given times. The number of ants feeding at bait was counted afteward from the pictures. In this example, 63 *T. nigerrimum* workers are feeding at bait.

a/ spring **b/ summer**

Figure 8.10 — *Las Beles* schrubland (Doñana National Park).

CHAPTER 9

Evolution of ant thermal preferences

9.1 Which constraints underpin the Dominance-Thermal tolerance trade-off?

In this part, different approaches to the study of foraging activity of Mediterranean ant species were proposed. The results emphasise the dependence of foraging intensity (chapters 6-7-8) and foraging distance (chapter 8) on ground temperature. Moreover, they demonstrate that this dependence differs between subordinate (*Aphaenogaster senilis*) and dominant species (*Tapinoma nigerrimum* , and *Lasius grandis*) of a Mediterranean ant community (chapters 7-8).

As explained by Dussutour et al. (2005), special collective behaviour might emerge either from an amplification of individual preferences or from a modification of the amplification process. Limitation of the foraging schedule in response to high temperature might thus result from either individual thermal preferences or from the failure of the communication system.

Some environmental factors, such as temperature, are known to affect ant colonies by acting as a constraint on the individual worker behaviour. As small poikilotherms, ants critically depend on temperature in their survival, growth, metabolism and mobility (Hölldobler and Wilson, 1990; Porter and Tschinkel, 1993; Fernández-Escudero et al., 1997; Penick and Tschinkel, 2008; Hurlbert et al., 2008). Besides, dominant ant species are physiologically less tolerant to stressful temperatures (Bestelmeyer, 1997; Cerdá et al., 1997; Wittman et al., 2010) explaining thereby the difference of foraging schedules. This was called the Dominance-Thermal tolerance trade-off. Nevertheless, the functional constraints supporting this trade-off are poorly understood.

In the discussion of his study, Bestelmeyer (2000) hypothesises the existence of a trade-off between the synthesis of two kinds of proteins. Since thermal tolerance is related to heat-shock protein synthesis (Gehring and Wehner, 1995), Bestelmeyer (2000) suggests a trade-off between the synthesis of these proteins and the chemicals used for defensive behaviour. No such trade-off has been yet identified. No evidences prove that an organism cannot both accumulate heat-shock proteins and produce an efficient trail pheromone. However, we demonstrated that high temperatures limit trail pheromone efficiency because of pheromone decay (chapters 6 & 7). In species whose foraging activity relies on chemical communication like dominants, the production of large quantities of heat shock proteins would thus be a cost without possible benefit. This hypothesis assumes that heat-shock proteins and trail pheromone synthesis are both costly for individuals.

The evolution of thermal foraging preferences is probably driven by the interplay between individual preferences and amplification possibilities. High temperatures negatively affect amplification processes in ants' collective foraging. This was demonstrated by heating the trail pheromone without exposing ants to high temperatures (chapters 6 & 7). Other mechanisms probably interfere at the amplification level. For instance, high temperature could also affect ants' ability to detect pheromone, or more probably ants' decision to lay pheromone. Further studies would be necessary to fully understand the "intelligent decision criteria" used by ants regarding ground temperature (Detrain and Deneubourg, 2002).

9.2 Critical thermal limits in ants: adaptation or acclimatization?

The critical thermal limits are parameters commonly used to measure the physiological tolerance of poikilotherms to stressful temperatures (see Lutterschmidt and Hutchinson (1997) for review). Heating protocols were initially employed in vertebrates (Fry, 1967). In insects, especially in ants, methodology was adapted to estimate these threshold temperatures of cold or heat torpor (Schumacher and Whitford, 1974; Kay and Whitford, 1978). Cerdá et al. (1997) used the term of Critical Thermal Maximum (CTM) to refer to the maximum physiological tolerance to hot temperatures. The CTM was defined as the temperature at which at least 50 % of the workers died or lost muscular co-ordination after 10 min of exposure. The CTM determination was based on a temperature ramp protocol by raising temperature by 2°C from 20°C to 60°C. At each temperature, twenty workers of a given species were placed 10 min on the surface of the hot plate (confined in open cylinders). The number of individuals loosing muscular co-ordination was counted, and the CTM estimated thereby.

During the experiment presented in chapter 8, colonies were connected to a foraging area whose ground temperature was the CTM of the species. Since I was surprised by the high number of workers foraging in these stressful conditions, I made a brief replication of Cerdá et al.'s experiment. The same protocol was employed (with a ramp temperature starting at the CTM value obtained by Cerdá et al. (1997)). The results were very different (Table 9.1). Many factors could lead these differences.

Table 9.1 — Comparison of the obtained values of Critical Thermal maximum (CTM) to those previously established by (Cerdá et al., 1997).

	Tapinoma nigerrimum	*Aphaenogaster Senilis*	*Lasius grandis*
Cerdá et al. (1997)	42°C	46°C	
Personal observation	48°C	54°C	46°C

The first explanation could be some technical differences in the protocol employed. I used the same electric Plactronic Selecta hot plate, and the very same open cylinders. Nevertheless, since experiments were not conducted in the same laboratory, many external factors could have influenced the experiment such as ambient temperature, humidity level, or light intensity. My experiments were conducted in room at 25±1°C with 35±10% relative humidity. Cerdá et al. (1997) did not control neither the air temperature nor the room humidity.

The differences could originate in the difference between populations. I tested ants from Doñana National Park (Huelva, south-west Spain) while Cerdá et al. (1997) used ants from Canet de Mar (Barcelona, north-east Spain). Could ants from Doñana be more resistant to high temperatures than ants from Barcelona?

There might also be seasonal differences. According to the age of ants, the resistance to hot temperature could be different. In this case, foragers collected in the field in spring or in summer might not have the same resistance. Besides, in many ant species, foraging tasks involve older workers (Hölldobler and Wilson, 1990). Workers taken outside (or inside) the nest might have more (or less) previous experience of heat. Since thermal resistance is linked to the synthesis and accumulation of heat shock proteins, prior experience to heat might favour thermal resistance (Gehring and Wehner, 1995), and younger workers might be less resistant to high temperatures.

An alternative hypothesis would be a fast adaptation of ants to global warming. My experiments were conducted in summer 2009 while Cerdá et al. (1997) estimated their CTM values more than ten years ago. It is doubtful though that evolutionary processes could have selected more resistant individuals so fast.

It might be pertinent to test these hypotheses in order to determine to what extent the CTM is a robust species-specific measure. Moreover, CTM measures should be completed by other analysis such as water loss, or respirometry (measures the rates of CO_2 emission and O_2 consumption rates) (Cerdá and Retana, 2000; Lighton and Turner, 2004). Robust and objective measures of biophysical limits are indeed essential to discuss how far the thermal limits can be considered the result of evolutionary processes.


"Discussion & Prospects"

CHAPTER 10

Concluding remarks

10.1 Methodology: diversity of approaches

This dissertation studies ant foraging behaviour from different and complementary perspectives combining theoretical work, experiments in controlled conditions, chemical analyses, and field work. This diversity of approaches allowed to explore complex situations and to test a large variety of hypotheses.

Mathematical modelling is a powerful tool to suggest coherent explanations. Theoretical studies allow to explicit hypotheses by making the logical link between assumptions and predictions. In this dissertation, both evolutionary (ultimate) and mechanistic (proximate) explanations were presented.

Chapters 3 & 4 presented evolutionary models based on population dynamics and mutation-selection processes. This theoretical approach is particularly suitable to examine possible evolutionary scenarios. In our particular case, they establish the conditions competitive trade-offs should fulfil to allow the emergence and persistence of strategy diversity. Our adaptive dynamics models link the long-term evolution of foraging behaviour to the short-term interactions between colonies and colony growth. They suggest that the Dominance-Discovery trade-off could explain the diversity of foraging strategies according to the intensity of asymmetric competition.

Chapter 6 presents a mechanistic model that was fitted to empirical data by Bayesian inference. This model suggests a link between collective foraging and ground temperature through pheromone dynamics. Specifically, it predicts that high temperatures accelerate trail pheromone evaporation and lead to a reduction of collective foraging efficiency.

In self-organised systems, models are usually based on differential equations and Monte Carlo simulations (Camazine et al., 2001). Dynamical processes are modelled as a set of ordinary or partial differential equations. Many studies propose an analytical resolution of dynamic systems (Nicolis and Deneubourg, 1999; Dussutour et al., 2004; Vincent A. D. and Myerscough M. R., 2004; Johnson and Rossi, 2006; Nicolis and Dussutour, 2008; Dussutour et al., 2009). Nevertheless, the stochasticity of self-organised processes is often better handled by Monte Carlo simulations (Deneubourg et al., 1990; Beckers, 1990; Fourcassié and Deneubourg, 1994; Nicolis et al., 2003; Vittori et al., 2004; Dussutour et al., 2004; Jeanson et al., 2007; Dussutour et al., 2009). Most of these studies determine empirically the parameters used in the simulations. However, when decision-making models fit both deterministic and stochastic processes to experimental data, Bayesian inference is a very convenient and statistically powerful tool to estimate parameters. Besides, algorithms such as JAGS (Just Another Gibbs Sampler, open-source engine for the Bayesian inference Using Gibbs Sampling (BUGS) language) (Plummer, 2009) allow both an accurate parameters estimation and Markov Chains Monte Carlo (MCMC) simulations. Random samples of the parameter are estimated from the data, and random simulations are computed.

A third kind of theoretical model could have pertinently completed the study presented in chapter 8. Stochastic dynamic optimisation models are appropriate to integrate state-dependent behaviour (McNamara and Houston, 1996). In particular, dynamic programming allows to establish fine-scale behavioural decisions that maximise fitness (Mangel and Clark, 1988; Houston et al., 1988a). In this framework, an animal is described by a set of variables characterising its state, a set of actions it can perform, and a reward function that specifies its future reproductive success in a short interval. Besides, frequency dependence might be included in the model in the form of dynamic games (McNamara and Houston, 1990). State-dependent theoretical studies might consider either the determination of the optimal choice of an isolated animal or its decision in a population of conspecifics using different strategies (Sirot and Bernstein, 1996). In our case, developing this kind of model might be convenient to propose possible adaptative explanations and to test their coherence with experimental data (Sirot et al., 1997).

Experiments under controlled conditions were performed in order to isolate the effect of temperature on ant behaviour. Two kinds of experiments were conducted: bioassays on trail pheromone efficiency (chapters 6 & 7) and behavioural experiments on state-dependent decisions (chapter 8).

Bioassays were conducted with an Y-shaped device. Ants had to choose between a branch previously marked by a trail pheromone either natural (chapter 6), or artificial (chapter 7), and an unmarked branch. The use of this method is particularly pertinent when a choice is necessary between two competing trails. In the second experiment for instance, it was necessary to control that the attractiveness of gaster extract was not due to the solvent. Notwithstanding, other types of bioassay could have been used such as a straight line test, or a circular trail (Pasteels and Verhaeghe, 1974). In those tests, the measure deals with the time passed or the distance covered on the trail by an individual. The circular trail, for instance, might be a pertinent test to establish the effect of time on pheromone decay. In an Y-shaped device, individuals that explore a given branch and do not find food might later switch to the second branch. Since circular trails never stop, individuals would not choose the opposite direction because of the absence of food, and the dynamics of pheromone efficiency could be better assessed.

Chemical analyses were conducted in order to identify the trail pheromone of *Tapinoma nigerrimum*, and to quantify the pheromone decay at the chemical level (chapter 7).

Chapter 7 presents a method to retrieve chemicals laid on a glass support. Glass surfaces are excellent adsorbers of pheromone that can easily be desorbed by solvent rinsing (Baker et al., 1980). Our protocol consisted in carefully rinsing a glass slide (where pheromone had been previously laid) with dichloromethane. This technique appeared effective since the quantity of each compound was similar between the extract and the control solutions (Fig. 7.8 & 7.10). Only the light Ketones were too volatile to be retrieved from the glass slide. However, as bioassays have showed, they are probably not an essential compound in the trail pheromone (Simon and Hefetz, 1991). Our technique is thus effective to retrieve trail pheromone laid on glass slides. It might be a method for chemical identification of trail components without killing ants for extraction. Moreover, this technique could be useful to assess what compounds are really laid by ant individuals and in which quantity.

Field work is an essential component of behavioural ecology since it provides direct information on what really occurs in natural settings. However, in field conditions, it is sometimes difficult to assess the causes of the observed patterns. For instance, concerning ant foraging activity, environmental parameters such as light intensity or temperature cannot be dissociated from circannual and circadian rhythm. Statistical analyses however allow to integrate both variables (chapter 6). In chapter 7, we chose to attribute all the variability of the foraging activity to the daily and seasonal rhythm in a first model, and to test the effect of temperature on the residuals of this model. Consistently with the result of chapter 6, the foraging activity of *Tapinoma nigerrimum* was highly dependent on temperature variations.

Conversely, temperature had no significant effect on the foraging activity of *Aphaenogaster senilis* . This does not mean that the activity of *A. senilis* was independent of temperature, but that temperature did not explain more variation in the foraging activity than did the circadian rhythm. The circadian rhythm is linked to temperature, but could also integrate other factors such as azimuthal position (F. Amor, *Unpublished data*).

Ant foraging activity is also dependent on competitive interactions. In chapter 8 for instance, we observed that the distance covered by the foragers of the subordinate species increased with ground temperature. Nevertheless, this pattern might be due either to an intrinsic thermophily, or to the control of baits by dominant species at low temperatures. To assess the extent to which competition affects the foraging activity of ant colonies, some field studies either remove (Gibb and Hochuli, 2004; Boulay et al., *In press.*) or enclose (Sanders and Gordon, 2000) competitors.

In field work, many other factors interfere with the studied variable, though this difficulty might remain the very interest of the field: it is real.

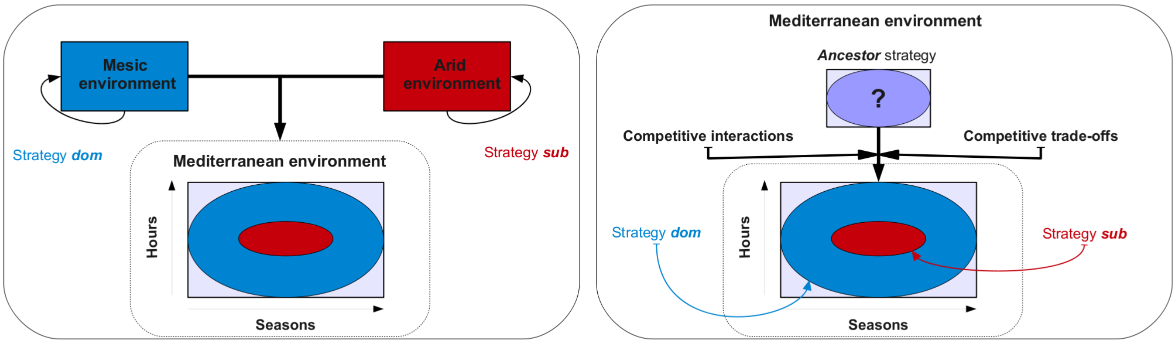
10.2 Insight into the evolution of ant communities

This thesis focused on ant foraging strategies. In many organisms, feeding activity is the most remarkable aspect of behaviour. In ants, foraging is the keystone of competitive interactions within a community. The study of foraging strategy evolution allows thereby to discuss the evolution of community structure.

Linking dominance with the degree of cooperation while foraging, we demonstrated that a single trade-off could explain the coevolution of different strategies. In this regard, independently of the ancestor strategy, all the diverging strategies would be "optimal" (Evolutionary stable). It would thus be misleading to refer to subordinates as species with a suboptimal strategy coexisting locally with dominants as fugitive species (Tanner and Adler, 2009).

Many studies documented that subordinate ant species are more tolerant to stressful temperatures than dominants (Cerdá et al., 1997, 1998a; Bestelmeyer, 1997, 2000; Lessard et al., 2009; Wittman et al., 2010). However, the evolutionary path that created ant communities structured by temperature remains poorly understood. Did stress tolerance evolve in response to competitive interactions or independently in arid habitats (Fig. 10.1)?

Even if this is probably an unsolvable question, theoretical studies could provide information on the plausibility of such scenarios. The modelling framework we used in the first part of this dissertation demonstrated that scenario 10.1b was theoretically possible. Adaptive Dynamics models could likewise determine the environmental characteristics (such as seasonal and daily temperature fluctuation) and on the competitive interactions that would



(a) Parallel evolution

(b) Coevolution

Figure 10.1 — Evolutionary scenarios for the evolution of Mediterranean ant communities. Scenario (a), parallel evolution: strategy *dom* (collective foraging and low thermal tolerance) evolved in mesic habitats while strategy *sub* (individual foraging and high thermal tolerance) evolved in arid habitats. In Mediterranean communities, high temperature variations both seasonally and daily allow species coexistence. Scenario (b), coevolution: strategy *dom* and *sub* evolved in the same habitat from competition pressures. Both strategies emerge as different investements in response to competitive trade-offs. The diagram illustrates the different niches defined by temperature according to seasonal (spring→summer→fall), and daily (morning→evening) variation. Such conceptual diagrams were inspired by Bucy and Breed (2006).

favour one scenario or the other.

This dissertation was organised around two essential trade-offs of ant communities: the Dominance-Discovery trade-off on the one hand, and the Dominance-Thermal Tolerance trade-off on the other. These competitive trade-offs were isolated in order to study their relevance in ant evolution. However, the whole evolutionary process is probably driven by many selective pressures, and several trade-offs might interact.

Competitive interactions interact with environmental variations (Dunson and Travis, 1991). Factors such as spatial heterogeneity (Tilman, 1982; Amarasekare, 2003; Bolker et al., 2003), or recurrent but unpredictable environmental fluctuations (Wiens, 1977) contribute to reduce competitive exclusion. The real scenario of community evolution might thus be somewhere between scenario 10.1a and 10.1b and species diversity might be driven both by competitive and by environmental pressure.

10.3 Ants: from communities to individuals

Ant communities are often likened to plant communities (Andersen, 1991). The two communities are structured by both competition and environmental variation (Tilman, 1982;

Hölldobler and Wilson, 1990). Moreover, the analogy between these communities can be extended to the organisms. Both ant colonies and plants can be considered as sessile organisms since they nest in a fixed place. Besides, both display equivalent foraging strategies with ramifying structures (López et al., 1994). Notwithstanding, to what extent can ant colonies be considered as modular organisms?

Ant colonies are not homogeneous since they are organised in castes of workers that are morphologically different and specialise in different tasks (Oster and Wilson, 1978). Division of labour is also based on age. As Hölldobler and Wilson (1990) observes "a principal difference between human beings and ants is that whereas we send our young men to war, they send their old ladies". Age and experience might also contribute to inter-worker neurological (Gronenberg et al., 1996) and chemical (Ichinose et al., 2005) differences.

If ants behave like molecules (Detrain and Deneubourg, 2006), ants are not molecules (Ratnieks and Reeve, 1992). They are not even genetically identical and workers' genetic diversity might influence collective patterns. For instance, differences in the temporal activity pattern of colonies are correlated with genetic diversity of workers within colonies (Wiernasz et al., 2008; Cole et al., 2010). Interindividual variation might have ecological and therefore evolutionary consequences. Individual differences, or "personality", can be selected (Dall et al., 2004), and might be particularly adaptive in group living organisms (Giraldeau and Caraco, 2000). As other organisms, ants have individual preferences (Mailleux et al., 2005). They respond to environmental stimuli according to their own state and their individual abilities, either based on genetics or previous experience. Some ants, for instance, get lost on a trail (Pasteels et al., 1986) but these "errors" introduce a form of "creativity" in a deterministic pattern that might be optimal for collective organisation (Deneubourg et al., 1983). In a nutshell, we still have a lot to learn about and from ants, and many research trails still need to be laid.

References

Abrams, P. (2001a). Adaptive dynamics: neither F nor G. *Evolutionary Ecology Research*, 3:369–373.

Abrams, P. A. (2001b). Describing and quantifying interspecific interactions: a commentary on recent approaches. *Oikos*, 94:209–218.

Abrams, P. A. (2006a). The effects of switching behavior on the evolutionary diversification of generalist consumers. *American Naturalist*, 168:645–59.

Abrams, P. A. (2006b). The prerequisites for and likelihood of generalist-specialist coexistence. *American Naturalist*, 167:329–342.

Abrams, P. A., Matsuda, H., and Harada, Y. (1993). Evolutionarily unstable fitness maxima and stable fitness minima of continuous traits. *Evolutionary Ecology*, 7:465–487.

Adler, F. R. (1999). The balance of terror: an alternative mechanism for competitive trade-offs and its implications for invading species. *American Naturalist*, 154:497–509.

Adler, F. R. and Gordon, D. M. (1992). Information collection and spread by networks of patrolling ants. *American Naturalist*, 140:373–400.

Adler, F. R., Lebrun, E. G., and Feener, Jr, D. H. (2007). Maintaining diversity in an ant community: modeling, extending, and testing the dominance-discovery trade-off. *American Naturalist*, 169:323–333.

Adler, F. R. and Mosquera, J. (2000). Is space necessary? interference competition and limits to biodiversity. *Ecology*, 81:3226–3232.

Agosti, D. and Johnson, N. (2005). Antbase. version (05/2005). [12608 species of Formicidae on 13th October 2010].

Akino, T. and Yamaoka, R. (1996). Purification of the trail pheromone of *Lasius fuliginosus* Latreille. *Japanese Journal of Applied Entomology and Zoolology*, 40:233–238.

Al-Khafaji, K., Tuljapurkar, S., Carey, J. R., and Page, R. E. (2009). Hierarchical demography: a general approach with an application to honey bees. *Ecology*, 90:556–566.

Albrecht, M. and Gotelli, N. (2001). Spatial and temporal niche partitioning in grassland ants. *Oecologia*, 126:134–141.

Alexander, R. D. (1974). The evolution of social behaviour. *Annual Review of Ecology and Systematics*, 5:325–383.

Ali, M., Morgan, E., Detrain, C., and Attygalle, A. (1988). Identification of a component of the trail pheromone of the ant *Pheidole pallidula* (Hymenoptera: Formicidae). *Physiological Entomology*, 13:257–265.

Amarasekare, P. (2002). Interference competition and species coexistence. *Proceedings, Biological sciences*, 269:2541–50.

Amarasekare, P. (2003). Competitive coexistence in spatially structured environments: a synthesis. *Ecology Letters*, 6:1109–1122.

Amarasekare, P., Hoopes, M. F., Mouquet, N., and Holyoak, M. (2004). Mechanisms of coexistence in competitive metacommunities. *American Naturalist*, 164:310–326.

Amor, F., Ortega, P., Cerdá, X., and Boulay, R. (2010). Cooperative prey-retrieving in the ant *Cataglyphis floricola*: an unusual short-distance recruitment. *Insectes Sociaux*, 57:91–94.

Andersen, A. (1991). *Ant-Plant interactions*, chapter Parallels between ants and plants: implications for community ecology, pages 539–558. Oxford University Press, Oxford.

Andersen, A. N. (1992). Regulation of "momentary" diversity by dominant species in exceptionally rich ant communities of the Australian seasonal tropics. *The American Naturalist*, 140:401–20.

Andersen, A. N. (1995). A classification of Austrailian ant communities, based on functional groups which parallel plant life-forms in relation to stress and disturbance. *Journal of Biogeography*, 22:15–29.

Andersen, A. N. (2008). Not enough niches: non-equilibrial processes promoting species coexistence in diverse ant communities. *Austral Ecology*, 33:211–220.

Anderson, C. (2001). The adaptive value of inactive foragers and the scout-recruit system in honey bee (*Apis mellifera*) colonies. *Behavioral Ecology*, 12:111–119.

Angulo, E., Caut, S., and Cerdá, X. (In Press). Scavenging in Mediterranean ecosystems: effect of the invasive Argentine ant. *Biological Invasion*.

Arnan, X., Rodrigo, A., and Retana, J. (2007). Uncoupling the effects of shade and food resources of vegetation on Mediterranean ants: an experimental approach at the community level. *Ecography*, 30:161–172.

Attygalle, A., Cammaerts, M.-C., Cammaerts, R., Morgan, E., and Ollett, D. (1986). Chemical and ethological studies of the trail pheromone of the ant *Manica rubida* (hymenoptera: Formicidae). *Physiological Entomology*, 11:125–132.

Attygalle, A., Kern, F., Huang, Q., and Meinwald, J. (1998a). Trail pheromone of the myrmicine ant *Aphaenogaster rudis* (hymenoptera: Formicidae). *Naturwissenschaften*, 85:38–41.

Attygalle, A. and Morgan, E. (1983). Trail pheromone of the ant *Tetramorium caespitum* L. *Naturwissenschaften*, 70:364–365.

Attygalle, A. and Morgan, E. (1984). Identification of trail pheromone of the ant *Tetramorium caespitum* l. (hymenoptera: Myrmicinae). *Journal of Chemical Ecology*, 10:1453–1468.

Attygalle, A., Mutti, A., Rohe, W., Maschwitz, U., Garbe, W., and Bestmann, H. (1998b). Trail pheromone from the pavan gland of the ant *Dolichoderus thoracicus* (smith). *Naturwissenschaften*, 85:275–277.

Attygalle, A., Steghaus-Kovac, S., Ahmad, V., Maschwitz, U., Vostrowsky, O., and Bestmann, H. (1991). Cis-isogeraniol, a recruitment pheromone of the ant *Leptogenys diminuta*. *Naturwissenschaften*, 78:90–92.

Attygalle, A.B.and Vostrowsky, O., Bestmann, H., Steghaus-Kovac, S., and Maschwitz, U. (1988). (3r,4s)-4-methyl-3-heptanol, the trail pheromone of the ant *Leptogenys diminuta*. *Naturwissenschaften*, 75:315–317.

Azcárate, F. M., Kovacs, E., and Peco, B. n. (2007). Microclimatic conditions regulate surface activity in harvester ants *Messor barbarus*. *Journal of Insect Behavior*, 20:315–329.

Baker, T., Cardé, R., and Miller, J. (1980). Oriental fruit moth pheromone component emission rates measured after collection by glass-surface adsorption. *Journal of Chemical Ecology*, 6:749–758.

Baroni Urbani, C. (1989). Phylogeny and behavioural evolution in ants, with a discussion of the role of behaviour in evolutionary processes. *Ethology, Ecology and Evolution*, 1:137–168.

Baroni Urbani, C. (1993). The diversity and evolution of recruitment behaviour in ants, with a discussion of the usefulness of parsimony criteria in the reconstruction of evolutionary histories. *Insectes Sociaux*, 40:233–260.

Basset, A. and Angelis, D. L. (2007). Body size mediated coexistence of consumers competing for resources in space. *Oikos*, 116:1363–1377.

Beckers, R. (1990). Collective decision making through food recruitment. *Insectes sociaux*, 37:258–267.

Beckers, R., Deneubourg, J., and Goss, S. (1992). Trail laying behaviour during food recruitment in the ant *Lasius niger* (l.). *Insectes Sociaux*, 39:59–72.

Beckers, R., Deneubourg, J., and Goss, S. (1993). Modulation of trail laying in the ant *Lasius niger* (hymenoptera: Formicidae) and its role in the collective selection of a food source. *Journal of Insect Behavior*, 6:751–759.

Beckers, R., Goss, S., Deneubourg, J., and Pasteels, J. (1989). Colony size, communication and ant foraging strategy. *Psyche*, 96:239–256.

Beekman, M. and Dussutour, A. (2009). *Food exploitation by Social Insect: Ecological, Behavioral and Theoretical Approaches*, chapter How to tell your mates - costs and benefits of different recruitment mechanisms, pages 105–124.

Beekman, M., Komdeur, J., and Ratnieks, L. W. (2003). Reproductive conflicts in social animals: who has the power? *Trends in Ecology and Evolution*, 18:277–282.

Beekman, M., Lingeman, R., Kleijne, F. M., and Sabelis, M. W. (1998). Optimal timing of the production of sexuals in bumblebee colonies. *Entomologia Experimentalis et Applicata*, 88:147–154.

Beekman, M., Sumpter, D. J., and Ratnieks, F. L. (2001). Phase transition between disordered and ordered foraging in Pharaoh's ants. *Proceedings of the National Academy of Sciences USA*, 98:9703–6.

Bernadou, A. and Fourcassié, V. (2005). Does substrate coarseness matter for foraging ants? an experiment with *Lasius niger* (hymenoptera: Formicidae). *Journal of Insect Physiology*, 54:534–542.

Bernard, F. (1983). *Les fourmis et leur milieu en France méditerranénne*. Encyclopédie Entomologique, 16, éditions Lechevalier, Paris.

Bernstein, R. A. (1975). Foraging strategies of ants in response to variable food density. *Ecology*, 56:213–219.

Berville, L., Hefetz, A., Lenoir, A., Renucci, M., Espadaler, X., Blight, O., Tirard, A., and Provost, E. (2010). Using chemical tools to discriminate *Tapinoma* species. 26th Annual Meeting of the International Society of Chemical Ecology.

Bestelmeyer, B. T. (1997). Stress tolerance in some Chacoan dolichoderine ants: implications for community organization and distribution. *Journal of Arid Environments*, 35:297–310.

Bestelmeyer, B. T. (2000). The trade-off between thermal tolerance and behavioural dominance in a subtropical south american ant community. *Journal of Animal Ecology*, 69:998–1009.

Bestmann, H., Janssen, E., Kern, F., Liepold, B., and Hölldobler, B. (1995). All-trans geranylgeranyl acetate and geranylgeraniol, recruitment pheromone components in the dufour gland of the ponerine ant *Ectatomma ruidum*. *Naturwissenschaften*, 82:334–336.

Bestmann, H., Kern, F., Schäfer, D., and Witschel, M. (1992). (r)-3,4-dihydroisocoumarins, a new class of ant trail phromone. *Angewandte Chemie*, 31:795–796.

Bestmann, H., Liepold, B., Kress, A., and Hofmann, A. (1999). (2s,4r,5s)-2,4-dimethyl-5-hexanolide: ants of different species *Camponotus* can distinguish the absolute configuration of their trail pheromone. *Chemistry - a European Journal*, 5:2984–2989.

Beugnon, G., Chagné, P., and Dejean, A. (2001). Colony structure and foraging behavior in the tropical ant, *Gigantiops destructor*. *Insectes Sociaux*, 48:347–351.

Biesmeijer, J. C. and de Vries, H. (2001). Exploration and exploitation of food sources by social insect colonies: a revision of the scout-recruit concept. *Behavioral Ecology and Sociobiology*, 49:89–99.

Billen, J., Beeckman, W., and Morgan (1992). Active trail pheromone compounds and trail following in the ant *Atta sexdens sexdens* (hymenoptera formicidae). *Ethology Ecology and Evolution*, pages 197–202.

Blatrix, R., Schulz, C., Jaisson, P., Francke, W., and Hefetz, A. (2002). Trail pheromone of ponerine ant *Gnamptogenys striatula*: 4-methylgeranyl esters from dufour's gland. *Journal of Chemical Ecology*, 28:2557–2567.

Blight, O., Provost, E., Renucci, M., Tirard, A., and Orgeas, J. (2010). A native ant armed to limit the spread of the Argentine ant. *Biological Invasions*, 12:1491–1497.

Blüthgen, N. and Fiedler, K. (2004). Competition for composition: lessons from nectar-feeding ant communities. *Ecology*, 85:1279–1485.

Bolker, B. M., Pacala, S. W., and Neuhauser, C. (2003). Spatial dynamics in model plant communities: what do we really know? *American Naturalist*, 162:135–148.

Bonabeau, E., Theraulaz, G., and Deneubourg, J. (1998a). Group and mass recruitment in ant colonies: the influence of contact rates. *Journal of Theoretical Biology*, 195:157–66.

Bonabeau, E., Theraulaz, G., and Deneubourg, J. (1998b). The synchronization of recruitment-based activities in ants. *Biosystems*, 45:195–211.

Bonabeau, E., Theraulaz, G., and Deneubourg, J.-L. (1996). Quantitative Study of the Fixed Threshold Model for the Regulation of Division of Labour in Insect Societies. *Proceedings, Biological Sciences*, 263:1565–1569.

Bonabeau, E., Theraulaz, G., Deneubourg, J.-L., Aron, S., and Camazine, S. (1997). Self-Organization in Social Insects. *Trends in Ecology and Evolution*, 12:188–193.

Boomsma, J. and Franks, N. (2006). Social insecs: from selfish genes to self organisation and beyond. *Trends in Ecology and Evolution*, 21:303–308.

Boomsma, J. J. and Grafen, A. (1991). Colony-level sex ratio selection in the eusocial Hymenoptera. *Journal of Evolutionary Biology*, 3:383–407.

Boulay, R., Cerdá, X., Simon, T., Roldan, M., and Hefetz, A. (2007a). Intraspecific competition in the ant emphCamponutus cruentatus: should we expect the "dear enemy" effect? *Animal Behaviour*, 74:985–993.

Boulay, R., Galarza, J., Chéron, B., Hefetz, A., Lenoir, A., van Oudenhove, L., and Cerdá, X. (In Press). Competition among phylopatric females regulates population size and affects resource allocation in an ant species dispersing by colony fission. *Ecology*.

Boulay, R., Hefetz, A., Cerdá, X., Devers, S., Francke, W., Twele, R., and Lenoir, A. (2007b). Production of sexuals in a fission-performing ant: dual effects of queen pheromones and colony size. *Behavioral Ecology and Sociobiology*, 61:1531–1541.

Bourke, A. F. G. and Chan, G. L. (1999). Queen-worker conflict over sexual production and colony maintenance in perennial social insects. *American Naturalist*, 154:417–426.

Bourke, A. F. G. and Ratnieks, F. L. W. (1999). Kin conflict over caste determination in social Hymenoptera. *Behavioral Ecology and Sociobiology*, 46:287–297.

Brand, J. and Mpuru, S. (1993). Dufour's gland and poison gland chemistry of the myrmicine ant, *Messor capensis* (mayr). *Journal of Chemical Ecology*, 19:1315–1321.

Brian, M. V., Clarke, R. T., and Jones, R. M. (1981). A numerical model of an ant society. *Journal of Animal Ecology*, 50:387–405.

Brooks, S. and Gelman, A. (1997). General methods for monitoring convergence of iterative simulations. *Journal of Computational and Graphical Statistics*, 7:434–455.

Brown, J. H., Gillooly, J. F., Allen, A. P., Savage, V. M., and West, G. B. (2004). Toward a metabolic theory of ecology. *Ecology*, 85:1771–89.

Brown, M. J. F. and Gordon, D. M. (2000). How resources and encounters affect the distribution of foraging activity in a seed-harvesting ant. *Behavioral Ecology and Sociobiology*, 47:195–203.

Brown J.H., Marquet, P., and Taper, M. (1993). Evolution of body size: consequences of an energetic definition of fitness. *American Naturalist*, 142:573–584.

Bucy, A. M. and Breed, M. D. (2006). Thermoregulatory trade-offs result from vegetation removal by a harvester ant. *Ecological Entomology*, 31:423–429.

Bulmer, M. G. (1981). Worker-queen conflict in annual social hymenoptera. *Journal of Theoretical Biology*, 93:239–251.

Bulmer, M. G. (1983). The significance of protandry in social Hymenoptera. *American Naturalist*, 121:540–551.

Bulmer, M. G. and Taylor, P. D. (1981). Worker-queen conflict and sex ratio theory in social hymenoptera. *Heredity*, 47:197–207.

Calcagno, V., Mouquet, N., Jarne, P., and David, P. (2006). Coexistence in a metacommunity: the competition-colonization trade-off is not dead. *Ecology Letters*, 9:897–907.

Camazine, S., Deneubourg, J.-L., Franks, N., Sneyd, J., Theraulaz, G., and Bonabeau, E. (2001). *Self-Organization in Biological Systems*. Princeton University Press.

Carpintero, S. and Reyes-López, J. (2008). The role of competitive dominance in the invasive ability of the Argentine ant (*Linepithema humile*). *Biological Invasions*, 10:25–35.

Carroll, C. R. and Janzen, D. H. (1973). Ecology of foraging by ants. *Annual Review of Ecology and Systematics*, 4:231–257.

Cassill, D. (2002). Yoyo-bang: a risk-aversion investment strategy by a perennial insect society. *Oecologia*, 132:150–158.

Cavill, G., Robertson, P., and Davies, N. (1979). An argentine ant aggregation factor. *Experentia*, 35:989–990.

Cerdá, X., Angulo, E., Boulay, R., and Lenoir, A. (2009). Individual and collective foraging decisions: a field study of worker recruitment in the gypsy ant *Aphaenogaster senilis*. *Behavioral Ecology and Sociobiology*, 63:551–562.

Cerdá, X., Bosch, J., Alsina, A., and Retana, J. (1988). Dietary spectrum and activity patterns of *Aphaenogaster senilis* (Hymenoptera: Formicidae). *Société entomologique de France.*, 24:69–75.

Cerdá, X. and Retana, J. (1994). Food exploitation patterns in two sympatric seed-harvesting ants (*Messor bouvieri* and *Messor capitatus*, hym. formicidae) from Spain. *Journal of Applied Entomology*, 117:268–277.

Cerdá, X. and Retana, J. (2000). Alternative strategies by thermophilic ants to cope with extreme heat: individual versus colony level traits. *Oikos*, 89:155–163.

Cerdá, X. and Retana, J. (In Prep). Bottom-up understanding of Mediterranean ant communities: from specific life traits to community organization.

Cerdá, X., Retana, J., Bosch, J., and Alsina, A. (1989). Exploitation of food resources by the ant *Tapinoma nigerrimum* (Hym., Formicidae). *Acta OEcologica*, 10:419–429.

Cerdá, X., Retana, J., and Cros, S. (1997). Thermal disruption of transitive hierarchies in Mediterranean ant communities. *Journal of Animal Ecology*, 66:363–374.

Cerdá, X., Retana, J., and Cros, S. (1998a). Critical thermal limits in Mediterranean ant species: Functional trade-off between mortality risk and foraging performance. *Functional Ecology*, 12:45–55.

Cerdá, X., Retana, J., and Cros, S. (1998b). Prey size reverses the outcome of interference interactions of scavenger ants. *Oikos*, 82:99–110.

Cerdá, X., Retana, J., and Manzaneda, A. (1998c). The role of competition by dominants and temperature in the foraging of subordinate species in Mediterranean ant communities. *Oecologia*, 117:404–412.

Champagnat, N., Ferrière, R., and Ben Arous, G. (2001). The Canonical Equation of Adaptive Dynamics : A Mathematical View. *Akadémiai Kiadó*, 2:73–83.

Chave, J., Muller-Landau, H. C., and Levin, S. A. (2002). Comparing classical community models: theoretical consequences for patterns of diversity. *American Naturalist*, 159:1–23.

Chong, K.-F. and Lee, C.-Y. (2009). Influences of temperature, relative humidity and light intensity on the foraging activity of field populations of the longlegged ant, *Anoplolepis gracilipes* (Hymenoptera: Fromicidae). *Sociobiology*, 54:531–539.

Christiansen, F. B. (1991). On the conditions for evolutionary stability for a continuously varying character. *American Naturalist*, 138:37–50.

Cole, B. J., Edwards, R., Holbrook, C. T., Holm, L., Heyward, J., and Wiernasz, D. C. (2008). Does foraging activity affect foraging success in the western harvester ant (Hymenoptera: Formicidae). *Annals of the Entomological Society af America*, 101:272–276.

Cole, B. J., Smith, A. A., Huber, Z. J., and Wiernasz, D. C. (2010). The structure of foraging activity in colonies of the harvester ant, *Pogonomyrmex occidentalis*. *Behavioral Ecology*, 21:337–342.

Coll, M., Hefetz, A., and Lloyd, H. (1987). Adnexal gland chemistry of *Messor ebeninus* forel (formicidae: Myrmicinae). *Zeitschrift für Naturforschung C.*, 42:1027–1029.

Collett, T. S., Dillmann, E., Giger, A., and Wehner, R. (1992). Visual landmarks and route following in desert ants. *Journal of Comparative Physiology A: Neuroethology, Sensory, Neural, and Behavioral Physiology*, 170:435–442.

Couzin, I. (2007). Collective minds. *Nature*, 445:715.

Crawley, M. J. (2002). *Statistical Computing*. Wiley, Chichester, U.K.

Cros, S., Cerdá, X., and Retana, J. (1997). Spatial and temporal pattern variations in the activity patterns of Mediterranean ant communities. *Ecoscience*, 4:269–278.

Cross, J., Byler, R., Ravid, U., Silverstein, R.M. adn Robinson, S., Baker, P., Jutsum, A., Cherrett, J., and De Oliveira, J. (1979). The major component of the trail pheromone of the leaf-cutting ant, *Atta sexdens rubropilosa* forel: 3-ethyl-2,5-dimethylpyrazine. *Journal of Chemical Ecology*, 5:187–203.

Cross, J., West, J., Silverstein, R., Jutsum, A., and Cherrett, J. (1982). Trail pheromone of the leaf-cutting ant, *Acromyrmex octospinosus* (reich), (formicidae: Myrmicinae). *Journal of Chemical Ecology*, 8:1119–1124.

Crozier, R. and Pamilo, P. (1996). *Evolution of Social Insect Colonies*. Oxford University Press.

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

Darwin, C. (1859). *On the Oringin of Species by Means of Natural Selection*. Dover Publications, Inc. Mineola, New York.

Darwin, C. (1871). *The Descent of Man, and Selection in Relation to Sex*. John Murray.

Davidson, D. (1998). Resource discovery versus resource domination in ants: a functional mechanism for breaking the trade-off. *Ecological Entomology*, 23:484–490.

Dawkins, R. (1976). *The Selfish Gene*. Oxford University Press.

de Biseau, J. and Pasteels, J. (2000). Response thresholds to recruitment signals and the regulation of foraging intensity in the ant *Myrmica sabuleti* (Hymenoptera, Formicidae). *Behavioral processes*, 48:137–148.

de Mazancourt, C. and Dieckmann, U. (2004). Trade-off geometries and frequency-dependent selection. *American Naturalist*, 164:765–778.

De Oliveira, J., Martinez, O., Carnieri, N., Vilela, E., and Reis (1990). Components of the trail pheromone of the leaf-cutting ants *Atta laevigata* f. smith and *Atta bisphaerica* forel (formicidae: Attini). *Annales de la Société Entomologique de France*, 19:145–154.

Dechaume-Moncharmont, F. X., Dornhaus, A., Houston, A. I., McNamara, J. M., Collins, E. J., and Franks, N. R. (2005). The hidden cost of information in collective foraging. *Proceedings of the Royal Society B: Biological Sciences*, 272:1689–95.

Deneubourg, J., Aron, S., Goss, S., Pasteels, J., and Duerinck, G. (1986). Random behaviour, amplification processes and number of participants: how they contribute to the foraging properties of ants. *Physica D*, 22:176–186.

Deneubourg, J.-L., Aron, S., Goss, S., and Pasteels, J. (1990). The Self-Organizing Exploratory Pattern of the Argentine Ant. *Journal of Insect Behavior*, 3:159–168.

Deneubourg, J. L. and Goss, S. (1989). Collective patterns and decision-making. *Ethology, Ecology and Evolution*, 1:295–311.

Deneubourg, J.-L., Pasteels, J.-M., and Verhaeghe, J.-C. (1983). Probabilistic Behaviour in Ants: A Strategy of Errors? *Journal of theoretical Biology*, 105:259–271.

Dercole, F. and Rinaldi, S. (2008). *Analysis of Evolutionary Processes*. Princteon University Press.

Detrain, C. and Deneubourg, J. (1997). Scavenging by Pheidole pallidula a key for understanding decision-making systems in ants. *Animal Behaviour*, 53:537–547.

Detrain, C. and Deneubourg, J. (2002). Complexity of environment and parsimony of decision rules in insect societies. *Biological Bulletin*, 202:268–74.

Detrain, C. and Deneubourg, J. (2006). Self-organized structures in a superorganism : do ants "behave" like molecules ? *Physics of Life Reviews*, 3:162–187.

Detrain, C., Natan, C., and Deneubourg, J. (2001). The influence of the physical environment on the self-organised foraging patterns of ants. *Naturwissenschaften*, 88:171–4.

Dieckmann, U. (1997). *The Dynamical Theory of Coevolution*. PhD thesis, Universiteit Leiden.

Dieckmann, U. and Doebeli, M. (1999). On the origin of species by sympatric speciation. *Nature*, 400:354–357.

Dieckmann, U. and Law, R. (1996). The dynamical theory of coevolution: a derivation from stochastic ecological processes. *Journal of Mathematical Biology*, 34:579–612.

Diekmann, O. (2004). A beginners guide to adaptive dynamics. *Banach Center Publications*, 63:47–86.

Do Nascimento, R., Morgan, E., Moreira, D., and Della Lucia, T. (1994). Trail pheromone of leaf-cutting ant *Acromyrmex subterraneus subterraneus* (forel). *Journal of Chemical Ecology*, 20:1719–1724.

Doebeli, M. and Dieckmann, U. (2000). Evolutionary branching and sympatric speciation caused by different types of ecological interactions. *American Naturalist*, 156:S77–S101.

Doebeli, M. and Dieckmann, U. (2003). Speciation along environmental gradients. *Nature*, 421:259–264.

Doebeli, M., Dieckmann, U., Metz, J., and Tautz, D. (2005). What we have also learned: adaptive speciation is theoretically plausible. *Evolution*, 59:691–695.

Dunson, W. A. and Travis, J. (1991). The role of abiotic factors in community organization. *The American Naturalist*, 138:1067–1091.

Dussutour, A., Deneubour, J.-L., and Fourcassié, V. (2005). Amplification of individual preferences in a social context: the case of wall-following in ants. *Proceedings of the Royal Society B*, 272:705–714.

Dussutour, A., Fourcassié, V., Helbing, D., and Deneubour, J.-L. (2004). Optimal traffic organization in ants under crowded condition. *Nature*, 428:70–73.

Dussutour, A., Nicolis, S. C., Shephard, G., Beekman, M., and Sumpter, D. J. T. (2009). The role of multiple pheromones in food recruitment by ants. *The journal of Experimental Biology*, 212:2337–2348.

Edwards, J. and Chambers, J. (1984). Identification and source of a queen-specific chemical in the pharaoh's ant, *Monomorium pharaonis* (l.). *Journal of Chemical Ecology*, 10:1731–1747.

El-Sayed, A. M. (2008). The Pherobase: Database of Insect Pheromones and Semiochemicals. <http://www.pherobase.com>.

Ellison, A. M. (2004). Bayesian inference in ecology. *Ecology Letters*, 7:509–520.

Eshel, I. (1983). Evolutionary and continuous stability. *Journal of Theoretical Biology*, 103:99–111.

Espadaler, X., Tartally, A., Schultz, R., Seifert, B., and Nagy, C. (2007). Regional trends and preliminary results on local expansion rate in the garden invasive ant *Lasius neglectus* (Hymenoptera, Formicidae). *Insectes Sociaux*, 54:293–301.

Evershed, R. and Morgan, E. (1983). The amounts of trail pheromone substances in the venom of workers of four species of attine ants. *Insect Biochemistry*, 13:469–474.

Evershed, R., Morgan, E., and Cammaerts, M. (1981). Identification of the trail pheromone of the ant *Myrmica rubra* l., and related species. *Naturwissenschaften*, 68:374–376.

Feener, D. H. (2000). Is the assembly of ant communities mediated by parasitoids? *Oikos*, 90:79–88.

Feener, D. H., Jacobs, L. F., and Schmidt, J. O. (1996). Specialized parasitoid attracted to a pheromone of ants. *Animal Behaviour*, 51:61–66.

Fellers, J. H. (1987). Interference and exploitation in a guild of woodland ants. *Ecology*, 68:1466–1478.

Fernández-Escudero, I., Tinaut, A., and Ruano, F. (1997). Ovarian maturation under cold winter conditions in a high-mountain ant (Hymenoptera: Formicidae). *Environmental Entomology*, 26:1373–1377.

Fisher, R. A. (1930). *The Genetical Theory of Natural Selection*. Oxford University Press.

Foster, K., Wenseleers, T., and Ratnieks, F. (2006). Kin selection is the key to altruism. *Trends in Ecology an Evolution*, 21:57–60.

Fourcassié, V. and Deneubourg, J. (1994). The dynamics of collective exploration and trail-formation in *Monomorium pharaonis*: experiment and model. *Physiological Entomology*, 19:291–300.

Fourcassié, V. and Oliveira, P. S. (2002). Foraging ecology of the giant Amazonian ant *Dinoponera gigantea* (Hymenoptera, Formicidae, Ponerinae): activity schedule, diet and spatial foraging patterns. *Journal of Natural History*, 36:2211–2227.

Franks, N. R. and Deneubourg, J. L. (1997). Self-organizing nest construction in ants: individual worker behaviour and the nest's dynamics. *Animal Behaviour*, 54(4):779–96.

Franks, N. R., Ireland, B., and Bourke, A. F. (1990). Conflicts, social economics and life history strategies in ants. *Behavioral Ecology and Sociobiology*, 27:175–181.

Franks, N. R. and Richardson, T. (2006). Teaching in tandem-running ants. *Nature*, 439:153.

Fry, F. (1967). *Thermobiology*, chapter Response of vertebrate poikilotherms to temperature, pages 375–409. London and New York: Academic Press.

Gause, G. F. (1934). *The struggle for existence*. Williams and Wilkins, Baltimore.

Gehring, W. J. and Wehner, R. (1995). Heat shock protein synthesis and thermotolerance in *Cataglyphis*, an ant from the Sahara desert. *Proceedings of the National Academy of Sciences USA*, 92:2994–2998.

Geisel, T. a. D. S. (1955). *On Beyond Zebra*. Random House.

Gelman, A. and Rubin, D. (1992). Inference from iterative simulation using multiple sequences. *Statistical Science*, 7:457–511.

Geritz, S., Kisdi, E., Meszéna, G., and Metz, J. (1998). Evolutionarily singular strategies and the adaptive growth and branching of the evolutionary tree. *Evolutionary Ecology*, 12:35–57.

Geritz, S. A., van der Meijden, E., and Metz, J. A. (1999). Evolutionary dynamics of seed size and seedling competitive ability. *Theoretical Population Biology*, 55:324–43.

Geritz, S. A. H. (1998). *The Evolutionary Significance of Variation in Seed Size*. PhD thesis, Universiteit Leiden.

Geritz, S. A. H., Kisdi, E., Meszéna, G., and Metz, J. A. J. (2004). Adaptive Dynamics of Speciation: Ecological Underpinnings. In Dieckmann, U., Doebeli, M., Metz, J., and Tautz, D., editors, *Adaptive Speciation*, pages 54–75. Cambridge University Press.

Geritz, S. A. H., Kisdi, E., and Yan, P. (2007). Evolutionary branching and long-term coexistence of cycling predators: Critical function analysis. *Theoretical Population Biology*, 71:424–435.

Gibb, H. and Hochuli, D. F. (2004). Removal experiment reveals limited effects of a behaviorally dominant species on ant assemblages. *Ecology*, 85:648–657.

Gillooly, J. F., Brown, J. H., West, G. B., Savage, V. M., and Charnov, E. L. (2001). Effects of size and temperature on metabolic rate. *Science*, 293:2248–51.

Gillooly, J. F., Hou, C., and Kaspari, M. (2010). Eusocial insects as superorganisms - Insights from metabolic theory. *Communicative and Integrative Biology*, 3:360–362.

Giraldeau, L.-A. and Caraco, T. (2000). *Social foraging theory.* Princeton, NJ: Princeton University Press.

Giraud, T., Pedersen, J. S., and Keller, L. (2002). Evolution of supercolonies: the argentine ants of southern europe. *Proceedings of the National Academy of Sciences USA*, 99:6075–6079.

Gómez, C., Casellas, D., Olivera, J., and Bas, J. M. (2003). Structure of ground-foraging ant assemblages in relation to lands-use change in the northwestern Mediterranean region. *Biodiversityand Conservation*, 12:2135–2146.

Gomez, C. and Espadaler, X. (1998). Seed dispersal curve of a Mediterranean myrmecochore: influence of ant size and the distance to nests. *Ecological Research*, 13:347–354.

Gordon, D. (2007). Control without hierarchy. *Nature*, 446:143.

Gordon, D. M. (1983). The relation recruitment rate to activity rhythms in the harcester ant, *Pogonomyrmex barbatus*. *Journal of Kansas Entomological Society*, 56:277–285.

Gordon, D. M. (1988). Group-level exploration tactics in fire ants. *Behaviour*, 104:162–175.

Gordon, D. M. (1991). Behavioral flexibility and the foraging ecology of seed-eating ants. *American Naturalist*, 138:379–411.

Gordon, D. M. (1992). How colony growth affects forager intrusion between neighboring harvester ant colonies. *Behavioral Ecology and Sociobiology*, 31:417–427.

Gordon, D. M. (1995). The expandable network of ant exploration. *Animal Behaviour*, 50:995–1007.

Gordon, D. M. (1996). The organization of work in social insect colonies. *Nature*, 380:121–124.

Goss, S., Deneubourg, J., Pasteels, J., and Josens, G. (1989). A model of noncooperative foraging in social insects. *American Naturalist*, 134:273–287.

Greene, A. (1984). Production schedules of vespine wasps - an empirical test of the bang-bang optimization model. *Journal of Kansas Entomological Society*, 57:545–568.

Greene, M. and Gordon, D. (2007a). How patrollers set foraging direction in harvester ants. *The American Naturalist*, 170:943–948.

Greene, M. and Gordon, D. (2007b). Interaction rate informs harvester ant task decisions. *Behavioural Ecology*, 18:451–455.

Gronenberg, W., Heeren, S., and Hölldobler, B. (1996). Age-dependent and task-related morphological changes in the brain and the mushroom bodies of the ant *Caponotus floridanus*. *Journal of Experimental Biology*, 199:2011–2019.

Haak, U., Hölldobler, B., and Bestmann, H. (2001). Species-specificity in trail pheromones and Dufour's gland contents of *Camponotus atriceps* and *C. floridanus* (Hymenoptera: Formicidae). *Chemoecology*, 11:67–73.

Hamilton, W. D. (1964a). The genetical evolution of social behaviour. I. *Journal of Theoretical Biology*, 7:1–16.

Hamilton, W. D. (1964b). The genetical evolution of social behaviour. II. *Journal of Theoretical Biology*, 7:17–52.

Hangartner, W. (1969). Structure and variability of the individual odor trail in *Solenopsis geminata* Fabr. (Hymenoptera, Formicidae). *Z. vergl. Physiologie*, 62:111–120.

Hefetz, A. and Lloyd, H. A. (1983). Identification of new components from anal glands of *Tapinoma simrothi*. *Journal of Chemical Ecology*, 9:607–613.

Herbers, J. M. (1981). Reliability Theory and Foraging by Ants. *J. Theor. Biol.*, 89:175–189.

Hofbauer, J. and Sigmund, K. (1998). *Evolutionary Games and Population Dynamics*. Cambridge University Press, Cambridge, UK.

Hölldobler, B. (1971). Recruitment behavior in *Camponotus socius* (hym. formicidae). *Journal of Comparative Physiology A: Neuroethology, Sensory, Neural, and Behavioral Physiology*, 75:123–142.

Hölldobler, B. (1995). The chemistry of social regulation: multicomponent signals in ant societies. *Proceedings of the National Academy of Sciences USA*, 92:19–22.

Hölldobler, B. and Carlin, N. F. (1987). Anonymity and specificity in the chemical communication signals of social insects. *Journal of Comparative Physiology A*, 161:567–581.

Hölldobler, B., Morgan, E., Oldham, N., and Liebig, J. (2001). Recruitment pheromone in the harvester ant genus *Pogonomyrmex*. *Journal of Insect Physiology*, 47:369–374.

Hölldobler, B., Oldham, N., Alpert, G., and Liebig, J. (2002). Predatory behavior and chemical communication in two metapone species (hymenoptera:formicidae). *Chemoecology*, 12:147–151.

Hölldobler, B. and Wilson, E. O. (1990). *The Ants*. Harvard University Press.

Holway, D. A. (1999). Competitive mechanisms underlying the displacement of native ants by the invasive argentine ant. *Ecology*, 80:238–251.

Holway, D. A., Suarez, A. V., and Case, T. J. (2002). Role of abiotic factors in governing susceptibility to invasion : a test with argentine ants. *Ecology*, 83:949–952.

Hou, C., Kaspari, M., Vander Zanden, H. B., and Gillooly, J. F. (2010). Energetic basis of colonial living in social insects. *Proceedings of the National Academy of Sciences USA*, 23:3634–3638.

Houston, A., Clark, C., McNamara, J., and Mangel, M. (1988a). Dynamic models in behavioural and evolutionary ecology. *Nature*, 332:29–34.

Houston, A., Schmid-Hempel, P., and Kacelnik, A. (1988b). Foraging strategy, worker mortality, and the growth of the colony in social insects. *American Naturalist*, 131(1):107–114.

Houston, A. I., McNamara, J. M., and Hutchinson, J. M. C. (1993). General Results concerning the Trade-Off between Gaining Energy and Avoiding Predation. *Philosophical Transaction of the Royal Society of London B*, 341:375–397.

Howard, J., Henneman, M., Cronin, G., Fox, J., and Hormiga, G. (1996). Conditioning of scouts and recruits during foraging by a leaf-cutting ant, *Atta colombica*. *Animal Behaviour*, 52:299–306.

Hurlbert, A. H., Ballantyne IV, F., and Powell, S. (2008). Shaking a leg and hot to trot: the effects of body size and temperature on running speed in ants. *Ecological Entomology*, 33:144–154.

Hutchinson, G. (1959). Homage to Santa Rosalia or Why are there so many kinds of animals? *American Naturalist*, 93:145–159.

Hutchinson, G. E. and MacArthur, R. H. (1959). A theoretical ecological model of size distribution among species of animals. *American Naturalist*, 93:117–125.

Huwyler, S., Grob, K., and Viscontini, M. (1975). The trail pheromone of the ant, *Lasius fuliginosus*: identification of six components. *Journal of Insect Physiology*, 21:299–304.

Ichinose, K., Cerdá, X., Cristidès, J.-P., and Lenoir, A. (2005). Detecting nestmate recognition patterns in the fission-performing ant *Aphaenogaster senilis*: a comparison of different indices. *Journal of Insect Behavior*, 18:633–650.

Jackson, B., Keegans, S., Morgan, E., Cammaerts, M.-C., and Cammaerts, R. (1990). Trail pheromone of the ant *Tetramorium meridionale*. *Naturwissenschaften*, 77:294–296.

Jackson, B., Wright, P., and Morgan (1989). 3-ethyl-2,5-dimethylpyrazine, a component of the trail pheromone of the ant *Messor bouvieri*. *Experientia*, 45:487–489.

Jackson, D. E., Martin, S. J., Ratnieks, F. L. W., and Holcombe, M. (2007). Spatial and temporal variation in pheromone composition of ant foraging trails. *Behavioral Ecology*, 18:444–450.

Jaffe, K. (1980). Theoretical analysis of the communication system for chemical mass recruitment in ants. *Journal of theoretical biology*, 84:589–609.

Jaffe, K. and Deneubourg, J.-L. (1992). On foraging, recruitment systems and optimum number of scouts in eusocial colonies. *Insectes Sociaux*, 39:201–213.

Jaffe, K. and Howse, P. (1979). The mass recruitment system of the leaf cutting ant, *Atta Cephalotes* (L.). *Animal Behaviour*, 27:930–939.

Jansen, V. A. and Mulder, G. S. (1999). Evolving biodiversity. *Ecology Letters*, 2:379–386.

Janssen, E., Bestmann, H., Hölldobler, B., and Kern, F. (1995). N,n-dimethyluracil and actinidine, two pheromones of the ponerine ant *Megaponera foetens* (fab.) (hymenoptera: Formicidae). *Journal of Chemical Ecology*, 21:1947–1955.

Janssen, E., Hölldobler, B., and Bestmann, H. (1999). A trail pheromone component of the african stink ant, *Pachycondyla (Paltothyreus) tarsata* fabricius (hymenoptera: Formicidae: Ponerinae). *Chemoecology*, 9:9–11.

Janssen, E., Hölldobler, B., Kern, F., Bestmann, H., and Tsuji, K. (1997a). Trail pheromone of myrmicine ant *Pristomyrmex pungens*. *Journal of Chemical Ecology*, pages 1025–1034.

Janssen, E., Übler, E., Bauriegel, L., Kern, F., Bestmann, H., Attygalle, A.B.and Steghaus-Kovac, S., and Maschwitz, U. (1997b). Trail pheromone of the ponerine ant *Leptogenys peuqueti* (hymenoptera: Formicidae): a multicomponent mixture of related compounds pheromones. *Naturwissenschaften*, 84:122–125.

Jeanson, R., Fewell, J. H., Gorelick, R., and Bertram, S. M. (2007). Emergence of increased division of labor as a function of group size. *Behavioral Ecology and Sociobiology*, 62:289–298.

Jeanson, R., Ratnieks, F. L. W., and Deneubourg, J.-L. (2003). Pheromone trail decay rates on different substrates in the Pharaoh's ant, Monomorium pharaonis. *Physiological Entomology*, 28:192–198.

Jessen, K. and Maschwitz, U. (1986). Orientation and recruitment behavior of the ponerine ant *Pachycondyla tesserinoda* (Emery): laying of individual-specific trails during tandem-running. *Behavioral Ecology and Sociobiology*, 19:151–155.

Johnson, K. and Rossi, L. F. (2006). A mathematical and experimental study of ant foraging trail dynamics. *Journal of Theoretical Biology*, 241:360–9.

Johnson, L. K., Hubbell, S. P., and Feener, D. H. (1987). Defense of food supply by eusocial colonies. *American Zoologist*, 27:347–358.

Jordan, R. and Blüthgen, N. (2007). No evidence for a dominance-discovery trade-off among *Formica pratensis* colonies (Hymenoptera: Formicidae). *Myrmecological News*, 10:7–10.

Kacelnik, A. (1993). Leaf-cutting ants tease optimal foraging theorists. *Trends in Ecology and Evolution*, 8:346–348.

Kacelnik, A. and Bateson, M. (1996). Risky theories - The effects of variance on foraging decisions. *American Zoologist*, 36:402–434.

Karlson, P. and Lüscher, M. (1959). "Pheromones": a new term for a class of biologically active substances. *Nature*, 183:55–56.

Kay, C. and Whitford, W. (1978). Critical thermal limits of desert honey ants: possible ecological implications. *Physiological Zoology*, 51:206–2213.

Keller, L. and Chapuisat, M. (2002). Eusociality and Cooperation. *Encyclopedia of Life Sciences*.

Kern, F. and Bestmann, H. (1993). Antennal electrophysiological responsiveness of the ponerine ant *Leptogenys diminuta* to trail and recruitment pheromones and its structure analogs. *Naturwissenschaften*, 80:424–427.

Kern, F., Klein, R., Janssen, E., Bestmann, H., Attygalle, A., Schafer, D., and Maschwitz, U. (1997). Mellein, a trail pheromone component of the ants *Lasius fuliginosus*. *Journal of Chemical Ecology*, 23:779–792.

Kisdi, E. (1999). Evolutionary Branching under Asymmetric Competition. *Journal of theoretical biology*, 197:149–162.

Kneitel, J. M. and Chase, J. M. (2004). Trade-offs in community ecology: linking spatial scales and species coexistence. *Ecology Letters*, 7:69–80.

Kohl, E., Hölldobler, B., and Bestmann, H. (2000). A trail pheromone component of the ant *Mayriella overbecki* viehmeyer (formicidae: Myrmicinae). *Naturwissenschaften*, 87:320–322.

Kohl, E., Hölldobler, B., and Bestmann, H. (2001). Trail and recruitment pheromones in *Camponotus socius* (Hymenoptera: Formicidae). *Chemoecology*, 11:67–73.

Kohl, E., Hölldobler, B., and Bestmann, H. (2003). Trail pheromones and Dufour gland contents in three *Camponotus* species (*C. castaneus*, *C. balzani*, *C. sericeiventris*: Formicidae, Hymenoptera). *Chemoecology*, 13:113–122.

Law, R., Marrow, P., and Dieckmann, U. (1997). On evolution under asymmetric competition. *Evolutionary Ecology*, 11:485–501.

Lebrun, E. G. (2005). Who is the top dog in ant communities? Resources, parasitoids, and multiple competitive hierarchies. *Oecologia*, 142:643–652.

Lebrun, E. G. and Feener, Jr, D. H. (2007). When trade-offs interact: balance of terror enforces dominance discovery trade-off in a local ant assemblage. *Journal of Animal Ecology*, 76:58–64.

LeBrun, E. G. and Feener Jr, D. H. (2002). Linked indirect effects in ant-phorid interactions: impacts on ants assemblage structure. *Oecologia*, 133:599–607.

Legendre, S. (2002). ZEN: Eco-evolutionary software. Technical report, Laboratoire d'écologie, École Normale Supérieure, Paris, France. (www.biologie.ens.fr/legendre/zen/zen.html).

Lenoir, A. (1979). Feeding behavior in young societies of the ant *Tapinoma erraticum*: trophallaxis and polyethism. *Insectes Sociaux*, 26:19–37.

Lenoir, A., Aron, S., Cerdá, X., and Hefetz, A. (2009). *Cataglyphis* desert ants: a good model for evolutionary biology in Darwin's anniversary year — A review. *Israel Journal of Entomology*, 39:1–32.

Lenoir, A., Benoist, A., Francke, W., Hefetz, A., Cerdá, X., and Boulay, R. (In prep). Recruitment and trail following behaviour in two *Aphaenogaster* ants.

Lenoir, A., Hefetz, A., Simon, T., and Soroker, V. (2001). Comparative dynamics of gestalt odour formation in two ant species *Camponotus fellah* and *Aphaenogaster senilis* (Hymenoptera: Formicidae). *Physiological Entomology*, 26:275–283.

Lenoir, A., Nowbahari, E., Quérard, L., Pondicq, N., and Delalande, C. (1990). Habitat exploitation and intercolonial relationship in the ant *Cataglyphis cursor* (hymenoptera: Formicidae). *Acta Oecologica*, 11:3–18.

Lessard, J.-P., Dunn, R. R., and Sanders, N. J. (2009). Temperature-mediated coexistence in temperate forest ant communities. *Insectes Sociaux*, 56:149–156.

Lester, P. J., Stringer, L. D., and Haywood, J. (2010). The role of resource dispersion in promoting the co-occurrence of dominant and subordinate species. *Oikos*, 119:659–668.

Lighton, J. and Turner, R. (2004). Thermolimit respirometry: an objective assessment of critical thermal maxima in two sympatric desert harvester ants, *Pogonomyrmex rugosus* and *P. californicus*. *Journal of Experimental Biology*, 207:1903–1913.

Lighton, J. R. B. and Feener, D. H. (1989). Water-loss rate and cuticular permeability in foragers of the desert ant *pogonomyrmex rugosus*. *Physiological Zoology*, 62:1232–1256.

Linksvayer, T. A. and Wade, M. J. (2005). The evolutionary origin and elaboration of sociality in the aculeate Hymenoptera: maternal effects, sibsocial effects, and heterochrony. *Quarterly Review of Biology*, 80:317–336.

Lioni, A. and Deneubourg, J. L. (2004). Collective decision through self-assembling. *Naturwissenschaften*, 91(5):237–41.

Lizon à l'Allemand, S. and Witte, V. (2010). A sophisticated, modular communication contributes to ecological dominance in the invasive ant *Anoplolepis gracilipes*. *Biological Invasions*, DOI 10.1007/s10530-010-9750-7.

Longhurst, C., Baker, R., and Howse, P. (1979). Termite predation by *Megaponera foetens* (fab.) (hymenoptera: Formicidae). coordination of raids by glandular secretions. *Journal of Chemical Ecology*, 5:703–719.

López, F., Fungairiño, S., Serrano, J., Acosta, F., and Reunanen, P. (1997). Alloethic efficiency in the patrolling networks of a polymorphic ant, *Tapinoma nigerrimum* (Hymenoptera: Formicidae). *Journal of Insect Behavior*, 10:115–127.

López, F., Serrano, J., and Acosta, F. (1994). Parallels between the foraging strategies of ants and plants. *Trends in Ecology and Evolution*, 9:150–153.

Lutterschmidt, W. and Hutchinson, V. (1997). The critical thermal maximum: history and critique. *Canadian Journal of Zoology*, 75:1561–1574.

MacArthur, R. and Levins, R. (1964). Competition, habitat selection, and character displacement in a patchy environment. *Proceedings of the National Academy of Sciences USA*, 51:1207–1210.

Macevicz, S. and Oster, G. (1976). Modeling Social Insect Populations II : Optimal Reproductive Strategies in Annual Eusocial Insect Colonies. *Behavioral Ecology and Sociobiology*, 1:265–282.

Mailleux, A., Deneubourg, J., and Detrain, C. (2000). How do ants assess food volume? *Animal Behaviour*, 59(5):1061–1069.

Mailleux, A., Deneubourg, J., and Detrain, C. (2003). How does colony growth influence communication in ants? *Insectes Sociaux*, 50:24–31.

Mailleux, A., Detrain, C., and Deneubourg, J. (2005). Triggering and persistence of trail-laying in foragers of the ant *Lasius niger*. *Journal of Insect Physiology*, 51:297–304.

Mailleux, A., Detrain, C., and Deneubourg, J. (2006). Starvation drives a threshold triggering communication. *Journal of Experimental Biology*, 209(Pt 21):4224–9.

Mangel, M. and Clark, C. (1988). *Dynamic Modeling in Behavioral Ecology*. Princeton University Press.

Marsh, A. C. (1985). Microclimatic factors influencing foraging patterns and success of the thermophilic desert ant, Ocymyrmex barbiger. *Insectes Sociaux*, 32:286–296.

Maynard Smith, J. (1974). The theory of games and the evolution of animal conflicts. *Journal of theoretical Biology*, 47:209–221.

Maysov, A. and Kipyatkov, V. E. (2009). Critical thermal minima, their spatial and temporal variation and response to hardening in Myrmica ants. *CryoLetters*, 1:29–40.

McDonough, L., Brown, D., and Aller, W. (1989). Insect sex pheromones: Effect of Temperature on Evaporation Rates of Acetates from Rubber Septa. *Journal of Chemical Ecology*, 15:779–790.

McNamara, J. and Houston, A. (1990). State-dependent ideal free distributions. *Evolutionary Ecology*, 4:298–311.

McNamara, J. and Houston, A. (1992). Risk-sensitive foraging: a review of the theory. *Bulletin of Mathematical Biology*, 54:355–378.

McNamara, J. and Houston, A. (1996). State-dependent life history. *Nature*, 380:215–221.

Meinwald, J., Wiemer, D., and Hölldobler, B. (1983). Pygidial gland secretions of the ponerine ant *Rhytidoponera metallica*. *Naturwissenschaften*, 70:46–47.

Metz, J., Geritz, S., Meszena, G., Jacobs, F., and van Heerwaarden, J. (1996). Adaptive dynamics: A geometrical study of the consequences of nearly faithful reproduction. In van Strien, S. and Verduyn Lunel, S., editors, *Stochastic and Spatial Structures of Dynamical Systems*, chapter Adaptive dynamics: A geometrical study of the consequences of nearly faithful reproduction, pages 183–231. North-Holland Publishing Co., Amsterdam, Netherlands.

Michener, C. D. and Brother, D. J. (1974). Were workers of eusocial Hymenoptera initially altruistic or oppressed? *Proceedings of the National Academy of Sciences USA*, 71:671–674.

Michod, R. (1999). *Darwinian Dynamics: Evolutionary Transitions in Fitness and Individuals*. Princeton, N.J.: Princeton University Press.

Mitesser, O., Weissel, N., Strohm, E., and Poethke, H. (2007a). Optimal investment allocation in primitively eusocial bees: a balance model based on resource limitation of the queen. *Insectes Sociaux*, 54:234–241.

Mitesser, O., Weissel, N., Strohm, E., and Poethke, H. J. (2006). The evolution of activity breaks in the nest cycle of annual eusocial bees: a model of delayed exponential growth. *BMC Evolutionary Biology*, 6:45.

Mitesser, O., Weissel, N., Strohm, E., and Poethke, H. J. (2007b). Adaptive dynamic resource allocation in annual eusocial insects: Environmental variation will not necessarily promote graded control. *BMC Ecology*, 7(1):16.

Moore, P. G. (1954). Spacing in plant populations. *Ecology*, 35:222–227.

Morgan, E., Brand, J., Mori, K., and Keegans, S. (2004). The trail pheromone of the ant *Crematogaster castanea*. *Chemoecology*, 14:119–120.

Morgan, E., Hölldobler, B., Vaisar, T., and Jackson, B. (1992). Contents of poison apparatus and their relation to trail-following in the ant *Daceton armigerum*. *Journal of Chemical Ecology*, 18:2161–2168.

Morgan, E., Jackson, B., Ollett, D., and Sales, G. (1990). Trail pheromone of the ant *Tetramorium impurum* and model compounds: structure-activity comparisons. *Journal of Chemical Ecology*, 16:3493–3510.

Morgan, E., Keegans, S., Tits, J., Wenseleers, T., and Billen (2006). Preferences and differences in the trail pheromone of the leaf-cutting ant *Atta sexdens sexdens* (hymenoptera: Formicidae). *European Journal of Entomology*, 103:553–558.

Morgan, E. and Ollett, D. (1987). Methyl 6-methylsalicylate, trail pheromone of the ant *Tetramorium impurum*. Naturwissenschaften. *Naturwissenschaften.*, 74:596–597.

Morgan, E. D. (2009). Trail pheromones of ants. *Physiological Entomology*, 34:1–17.

Nanjundiah, V. (2010). Evolution of social behaviour. Available from Nature Precedings <http://hdl.handle.net/10101/npre.2010.4941.1>.

Nicolis, S. and Deneubourg, J. (1999). Emerging patterns and food recruitment in ants: an analytical study. *Journal of Theoretical Biology*, 198(4):575–92.

Nicolis, S. C., Detrain, C., Demolin, D., and Deneubourg, J. L. (2003). Optimality of collective choices: a stochastic approach. *Bulletin of Mathematical Biology*, 65(5):795–808.

Nicolis, S. C. and Dussutour, A. (2008). Self-organization, collective decision making and resource exploitation strategies in social insects. *The European Physical Journal B*, 65(5):379–385.

Nonacs, P. (1990). Death in the distance: mortality risk as information for foraging ants. *Behaviour*, 112:23–35.

Nonacs, P. and Calabi, P. (1992). Competition and predation risk: their perception alone affects ant colony growth. *Proceedings of the Royal Society of London B*, 249:95–99.

Nonacs, P. and Dill, L. (1990). Mortality risk vs. food quality trade-offs in a common currency: ant patch preferences. *Ecology*, 71:1886–1892.

Nonacs, P. and Dill, L. (1991). Mortality risk versus food quality trade-offs in ants: patch use over time. *Ecological Entomology*, 16:73–80.

Nowak, M. A. (2006). Five rules for the evolution of cooperation. *Science*, 314:1560–1563.

Nowak, M. A., Tarnita, C. E., and Wilson, E. O. (2010). The evolution of eusociality. *Nature*, 466:1057–1062.

Ntzoufras, I. (2009). *Bayesian modeling using WinBugs*. John Wiley and Sons, Inc., Hoboken, New Jersey.

Ohtsuki, H. and Tsuji, K. (2009). Adaptive reproduction schedule as a cause of worker policing in social Hymenoptera: a dynamic game analysis. *The American Naturalist*, pages 747–758.

Oldham, N., Morgan, E., Gobin, B., and Billen, J. (1994). First identification of a trail pheromone of an army ant (*Aenictus* species). *Experientia*, 50:763–765.

Ono, T. (1993). Effect of rearing temperature on pheromone component ratio in potato tuberworm moth, *Phthorimaea operculella*, (Lepidoptera: Gelechiidae). *Journal of Chemical Ecology*, 19:71–81.

Oster, G. F. and Wilson, E. O. (1978). *Caste and ecology in the social insects.* Princeton University Press.

Palmer, T. M., Young, T. P., Stanton, M. L., and Wenk, E. (2000). Short-term dynamics of an acacia ant community in Laikipia, Kenya. *Oecologia*, 123:425–435.

Pamilo, P. (1991). Evolution of colony characteristics in social insects. II. Number of reproductive individuals. *The American Naturalist*, 138(2):412–433.

Park, T. (1962). Beetles, competition and population. *Science*, 138:1369–1375.

Parr, C., Sinclair, B., Andersen, A., Gaston, K., and Chown, S. (2005). Constraint and competition in assemblages: a cross-continental and modeling approach for ants. *American Naturalist*, 165:481–494.

Parr, C. L. and Gibb, H. (2010). Competition and the role of dominant ants. In Lach, L., Parr, C. L., and Abbott, K. L., editors, *Ant Ecology*, chapter Competition and the role of dominant ants, pages 77–96. Oxford University Press, Oxford.

Pasteels, J., Deneubourg, J., Verhaeghe, J., Boevé, J., and Quinet, Y. (1986). *Mechanisms in insect olfaction*, chapter Orientation along terrestrial trails by ants, pages 131–138. Oxford : Clarendon.

Pasteels, J. and Verhaeghe, J. (1974). Dosage biologique de la phéromone de piste chez les fourrageuses et les reines de *Myrmica rubra*. *Insectes sociaux*, 21:167–180.

Pavan, M. and Trave, R. (1958). Étude sur les Formicidae. IV. Sur le venin du Dolichodéride *Tapinoma nigerrimum* Nyl. *Insectes Sociaux*, 5:299–308.

Pearce, J. M. C. (2008). *Fast food: the mechanisms of resource discovery in ant communities*. PhD thesis, University of Utah.

Pearce-Duvet, J. M. C. and Feener, D. H. (2010). Resource discovery in ant communities: do food type and quantity matter? *Ecological Entomology*, 35:549–556.

Penick, C. A. and Tschinkel, W. R. (2008). Thermoregulatory brood transport in the fire ant, *Solenopsis invicta*. *Insectes Sociaux*, 55:176–182.

Perfecto, Y. (1994). Foraging behavior as a determinant of asymmetric competitive interaction between two ant species in a tropical agroecosystem. *Oecologia*, 98:184–192.

Planqué, R., van den Berg, J. B., and Franks, N. R. (2010). Recruitment strategies and colony size in ants. *Plos One*, 5:1–8.

Plummer, M. (2009). rjags: Bayesian graphical models using mcmc. *R package version 1.0.3-12*, http://CRAN.R-project.org/package=rjags.

Poitrineau, K., Mitesser, O., and Poethke, H. J. (2009). Workers, sexuals, or both? Optimal allocation of resources to reproduction and growth in annual insect colonies. *Insectes Sociaux*, 56:119–129.

Pol, R. and Lopez de Casenave, J. (2004). Activity patterns of Harvester Ants *Pogonomyrmex pronotalis* and *Pogonomyrmex rastratus* in the central monte desert, Argentina. *Journal of Insect Behaviour*, 17:647–661.

Pontryagin, L., Boltyanskii, V., Gamkrelidaze, R., and Mischenko, E. (1962). *The Mathematical Theory of Optimal Processes*. New York: John Wiley and Sons.

Porter, S. D. and Tschinkel, W. R. (1993). Fire ant thermal preferences: behavioral control of growth and metabolism. *Behavioral Ecology and Sociobiology*, 32:321–329.

Portha, S., Deneubourg, J., and Detrain, C. (2002). Self-organized asymmetries in ant foraging: a functional response to food type and colony needs. *Behav Ecol*, 13:776–781.

Portha, S., Deneubourg, J., and Detrain, C. (2004). How food type and brood influence foraging decisions of *Lasius niger* scouts. *Animal Behaviour*, 68:115–122.

Putyatina, T. S. (2007). The choice of foraging strategy as a mechanism for the coexistence of *Myrmica* species (Hymenoptera, Formicidae) in a multispecific ant association. *Zoologicheskii Zhurnal*, 86:701–708.

Queller, D. C. and Strassmann, J. E. (1998). Kin selection and social insects. *Bioscience*, 48:165–175.

R Development Core Team (2010). *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0.

Ratnieks, F. L. W. and Reeve, H. K. (1992). Conflict in single-queen hymenopteran societies: the structure of conflict and processes that reduce conflict in advanced eusocial species. *Journal of Theoretical Biology*, 158:33–65.

Retana, J. and Cerdá, X. (1995). Agonistic relationship among sympatric Mediterranean ant species (Hymenoptera: Formicidae). *Journal of Insect Behaviour*, 8:365–380.

Retana, J. and Cerdá, X. (2000). Patterns of diversity and composition of Mediterranean ground ant communities tracking spatial and temporal variability in the thermal environment. *Oecologia*, 123:436–444.

Reuter, M. and Keller, L. (2001). Sex ratio conflict and worker production in eusocial hymenoptera. *American Naturalist*, 158:166–77.

Riley, R., Silverstein, R., Carroll, B., and Carroll, R. (1974). Methyl 4-methylpyrrole-2-carboxylate: a volatile trail pheromone from the leaf-cutting ant, *Atta cephalotes*. *Journal of Insect Physiology*, 20:651–654.

Ritter, F., Bruggemann Rotgans, I., Verwiel, P., Persoons, C., and Talman, E. (1977). Trail pheromone of the pharaoh's ant, *Monomorium pharaonis*: isolation and identification of faranal, a terpenoid related to juvenile hormone ii. *Tetrahedron Letters*, 30:2617–2618.

Robinson, E., Green, K., Jenner, E., Holcombe, M., and Ratnieks, F. (2008). Decay rates of attractive and repellent pheromones in an ant foraging trail network. *Insectes Sociaux*, 55:246–251.

Robinson, E. J., Jackson, D. E., Holcombe, M., and Ratnieks, F. L. W. (2005). "No entry" signal in ant foraging. *Nature*, 24:438–442.

Robinson, S. and Cherrett, J. . (1978). The possible use of methyl 4-methylpyrrole-2-carboxylate, an ant trail pheromone, as a component of an improved bait for leaf-cutting ant (Hymenoptera: Formicidae). *Bulletin of Entomological Research*, 68:159–170.

Roces, Flavio Hölldobler, B. (1994). Leaf density and a trade-off between load-size selection and recruitment behavior in the ant *Atta cephalotes*. *Oecologia*, 97(1):1–8.

Ruano, F., Tinaut, A., and Soler, J. J. (2000). High surface temperatures select for individual foraging in ants. *Behavioral Ecology*, 11:396–404.

Rueffler, C., Van Dooren, T. J., Leimar, O., and Abrams, P. A. (2006). Disruptive selection and then what? *Trends in Ecology and Evolution*, 21:238–245.

Sanders, N. J. and Gordon, D. (2000). The effects of interspecific interactions on resource use and behavior in a desert ant. *Oecologia*, 125:436–443.

Sanders, N. J. and Gordon, D. (2003). Resource-dependent interactions and the organization of desert ant communities. *Ecology*, 84:1024–1031.

Sanders, N. J., Gotelli, N. J., Wittman, S. E., Ratchford, J. S., Ellison, A. M., and Jules, E. S. (2007). Assembly rules of ground-foraging ant assemblages are contingent on disturbance, habitat and spatial scale. *Journal of Biogeography*, 34:1632–1641.

Santini, G., Tucci, L., Ottonetti, L., and Frizzi, F. (2007). Competition trade-offs in the organisation of a Mediterranean ant assemblage. *Ecological Entomology*, 32:319–326.

Savolainen, R. and Vepsäläinen, K. (1988). A competition hierarchy among boreal ants: impact on resource partitioning and community structure. *Oikos*, 51:135–155.

Savolainen, R. and Vepsäläinen, K. (1989). Niche differentiation of ant species within territories of the wood ant *Formica polyctena*. *Oikos*, 56:3–16.

Schmid-Hempel, P. (1990). Reproductive competition and the evolution of work load in social insects. *American Naturalist*, 135(4):501–526.

Schoener, T. W. (1971). Theory of feeding strategies. *Annual Review of Ecology and Systematics*, 2:369–404.

Schoener, T. W. (1983). Field experiments on interspecific competition. *American Naturalist*, 122:240–245.

Schumacher, A. and Whitford, W. (1974). The foraging ecology of two species of Chihuahuan desert ants: *Formica perpilosa* and *Trachyrmyrmex smithi neomexicanus* (Hymenoptera Formicidae). *Insectes Sociaux*, 21:317–330.

Simon, T. and Hefetz, A. (1991). Trail-following responses of *Tapinoma simrothi* (Formicidae: Dolichoderinae) to pygidial gland extracts. *Insectes Sociaux*, 38:17–25.

Sirot, E. and Bernstein, C. (1996). Time sharing between host searching and food searching in parasitoids: State-dependent optimal strategies. *Behavioural Ecology*, 7(2):189–194.

Sirot, E., Ploye, H., and Bernstein, C. (1997). State dependent superparasitism in a solitary parasitoid: Egg load and survival. *Behavioural Ecology*, 8(2):226–232.

Sober, E. (1984). *The Nature of Selection - Evolutionary Theory in Philosophical Focus*. MIT Press, Cambridge, MA.

Sonnet, P. and Moser, J. (1972). Synthetic analogs of the trail pheromone of the leaf-cutting ant, *Atta texana* (buckley). *Journal of Agricultural and Food Chemistry*, 20:1191–1194.

Sorvari, J. and Hakkarainen, H. (2007). The role of food and colony size in sexual offspring production in a social insect: an experiment. *Ecological Entomology*, 32:11–14.

Spiegelhalter, D., Best, N., Gilks, W., and Inskip, H. (1996). *Markov Chain Monte Carlo in Practice*. Chapman and Hall, London.

Stephens, D. W. and Krebs, J. R. (1986). *Foraging theory*. Princeton University Press, Princeton.

Stringer, L. D., Haywood, J., and Lester, P. J. (2007). The influence of temperature and fine-scale resource distribution on resource sharing and domination in an ant community. *Ecological Entomology*, 32:732–740.

Sudd, J. H. and Franks, N. R. (1987). *The Behavioural Ecology of Ants*. Chapman and Hall, New York.

Sumpter, D. (2006). The principles of collective animal behaviour. *Philosophical Transaction of the Royal Society B*, 361:5–22.

Sumpter, D. and Beekman, M. (2003). From nonlinearity to optimality: pheromone trail foraging by ant. *Animal Behaviour*, 66:273–280.

Sumpter, D. J. T. and Pratt, S. C. (2003). A modelling framework for understanding social insect foraging. *Behavioral Ecology and Sociobiology*, 53:131–144.

Tanner, C. J. (2008). Resource characteristics and competition affect colony and individual foraging strategies of the wood ant *Formica integroides*. *Ecological Entomology*, 33:127–136.

Tanner, C. T. and Adler, F. R. (2009). To fight or not to fight: context-dependent interspecific aggression in competing ants. *Animal Behaviour*, 77:297–305.

Tentschert, J., Bestmann, H., Hölldobler, B., and Heinze, J. (2000). 2,3-dimethyl-5-(2-methylpropyl)pyrazin, a trail pheromone component of *Eutetramorium mocquerysi* emery (1899) (hymenoptera: Formicidae). *Naturwissenschaften*, pages 377–380.

Theraulaz, G., Bonabeau, E., and Deneubourg, J. (1998). Response threshold reinforcement and division of labour in insect societies. *Proceedings of the Royal Society of London B*, 265:327–332.

Theraulaz, G., Gautrais, J., Camazine, S., and Deneubourg, J. (2003). The formation of spatial patterns in social insects: from simple behaviours to complex structures. *Philosophical Transaction A*, 361(1807):1263–82.

Thomas, M. and Holway, D. (2005). Condition-specific competition between invasive argentine ants and australian *Iridomyrmex*. *Journal of Animal Ecology*, 74:532–542.

Tilman, D. (1982). *Resource competition and community structure*. Princeton University Press.

Tilman, D. (1994). Competition and biodiversity in spatially structured habitat. *Ecology*, 75:2–16.

Torres, J. A. (1984). Niches and coexistence of ant communities in puerto rico: repeated patterns. *Biotropica*, 16:284–295.

Traniello, J. F. A. (1989). Foraging strategies of ants. *Annual Review of Entomology*, 34:191–210.

Traulsen, A. and Nowak, M. A. (2006). Evolution of cooperation by multilevel selection. *Proceedings of the National Academy of Sciences USA*, 103:10952–10955.

Tregenza, T. and Butlin, R. K. (1999). Speciation without isolation. *Nature*, 400:311–312.

Trivers, R. L. and Hare, H. (1976). Haplodiploidy and the evolution of the social insects. *Science*, 191:249–263.

Tumlinson, J., Moser, J., Silverstein, R., Brownlee, R., and Ruth, J. (1972). A volatile trail pheromone of the leaf-cutting ant, *Atta texana*. *Journal of Insect Physiology*, 18:809–814.

Uebler, E., Kern, F., Bestmann, H., Hölldobler, B., and Attygalle, A. (1995). Trail pheromone of two formicine ants, *Camponotus silvicola* and *C. rufipes* (hymenoptera: Formicidae). *Naturwissenschaften*, 82:523–525.

Van der Meer, R. (1983). Semiochemicals and the red imported fire ant (*Solenopsis invicta* Buren) (Hymenoptera: Formicidae). *Fla. Entomol.*, 66:139–161.

Van der Meer, R., Alvare, F., and Lofgren, C. (1988). Isolation of the trail recruitment pheromone of *Solenopsis invicta*. *Journal of Chemical Ecology*, 14:825–838.

Van der Meer, R., Williams, F. D., and Lofgren, C. (1981). Hydrocarbon components of the trail pheromone of the red imported fire ant, *Solenopsis invicta*. *Tetrahedron Letters*, 22:1651–1654.

van Dooren, T., Durinx, M., and Demon, I. (2004). Sexual dimorphism or evolutionary branching. *Evolutionary Ecology Research*, 6:857–871.

van Doorn, G. S., Dieckmann, U., and Weissing, F. J. (2004). Sympatric speciation by sexual selection: a critical reevaluation. *American Naturalist*, 163:709–725.

Van Vorhis Key, S. and Baker, T. (1982). Trail-following responses of the Argentine ant *Iridomyrmex humilis* (Mayr), to a synthetic trail pheromone component and analogs. *Journal of Chemical Ecology*, 8:3–14.

Vepsäläinen, K. and Pisarski, B. (1982). Assembly of island ant communities. *Annales Zoologici Fennici*, 19:327–335.

Vepsäläinen, K. and Savolainen, R. (1990). The effect of interference by formicine ants on the foraging of *Myrmica*. *Journal of Animal Ecology*, 59:643–654.

Vincent, T. and Brown, J. (2005). *Evolutionary Game theory, Natural Selection, and Darwinian Dynamics*. Cambridge University Press, Cambridge, UK.

Vincent A. D. and Myerscough M. R. (2004). The effect of a non-uniform turning kernel on ant trail morphology. *Journal of Mathematical Biology*, 49:391–432.

Vittori, K., Gautrais, J., Araujo, A. F. R., Fourcassié, V., and Theraulaz, G. (2004). Modeling Ant Behavior Under a Variable Environment. *Lecture notes in computer sciences*, 3172:190–201.

Volterra, V. (1931). *Leçons sur la théorie mathématique de la lutte pour la vie*. Gauthier-Villars, Paris.

von Frisch, K. (1967). *The dance language and orientation of bees*. Cambridge, MA: The Belknap Press of Harvard University Press.

Wade, M. J. (2001). Maternal effect genes and the evolution of sociality in haplo-diploid organisms. *Evolution*, 35:844–858.

Wehner, R. and Räber, F. (1979). Visual spatial memory in desert ants, *Cataglyphis bicolor* (Hymenoptera: Formicidae). *Cellular and Molecular Life Sciences*, 35:1569–1571.

West-Eberhard, M. J. (1986). Alternative adaptations, speciation, and phylogeny (A Review). *Proceedings of the National Academy of Sciences USA*, 83:1388–1392.

Wetterer, J. (2006). Quotation error, citation copying, and ant extinctions in Madeira. *Scientometrics*, 67:351–372.

Wetterer, J., Espadaler, X., Wetterer A.L., Aguin-Pombo, D., and Franquinho-Aguiar, A. (2006). Long-term impact of exotic ants on the native ants of Madeira. *Ecological Entomology*, 31:358–368.

Wheeler, W. M. (1911). The ant-colony as an organism. *Journal of Morphology*, 22:307–325.

Whitford, W. G. and Bryant, M. (1979). Behavior of a predator and its prey: the horned lizard (*Phrynosoma cornutum*) and the harvester ants (*Pogomyrmex* spp.). *Ecology*, 60:686–694.

Wiener, N. (1961). *Cybernetics: or Control and Communication in the Animal and the Machine*. Massachusetts Institute of Technology.

Wiens, J. A. (1977). On Competition and Variable Environments. *American Scientist*, 65:590–597.

Wiernasz, D., Hines, J., Parker, D., and Cole, B. (2008). Mating for variety increases colony activity in the harvester ant emphPogonomyrmex occidentalis. *Molecular Ecology*, 17:1137–1144.

Williams, H., Strand, M., and Vinson, S. (1981). Trail pheromone of the red imported fire ant *Solenopsis invicta* (buren). 37:1159–1160.

Wilson, D. and Sober, E. (1989). Reviving the superorganism. *Journal of Theoretical Biology*, 136:337–356.

Wilson, E. O. (1959). Communication by tandem running in the ant genus *Cardiocondyla*. *Psyche*, 66:29–34.

Wilson, E. O. (1971). *The insect societies*. Belknap University Press, Cambridge.

Wilson, E. O. (2008). One giant leap: how insects achieved altruism and colonial life. *BioScience*, 58:17–25.

Wilson, E. O. and Hölldobler, B. (2005). Eusociality: Origin and consequences. *PNAS*, 102:13367–13371.

Wittman, S. E., Sanders, Nathan, J., Ellison, A. M., Jules, E. S., Ratchford, J. S., and Gotelli, N. J. (2010). Species interactions and thermal constraints on ant community structure. *Oikos*, 119:551–559.

Wolf, T. J. and Schimd-Hemped, P. (1990). On the integration of individual foraging strategies with colony ergonomics in social insects: nectar-collection in honeybees. *Behavioral Ecology and Sociobiology*, 27:103–111.

*

APPENDIX A

Trail pheromone composition in ants

The following table presents a review of the currently identified trail pheromone in ants (see Morgan (2009) and El-Sayed (2008) for more details). For each described species, the compounds known to be involved in the trail pheromone are listed and the authorities cited. Some complementary information about the chemical compounds are provided such as the functional group, the chain length and the molecular weight.

Trail pheromone composition

GENUS	SPECIES	CHEMICAL COMPOUNDS	FUNCTIONAL GROUP	CHAIN LENGTH	MOLECULAR WEIGHT	REFERENCES
Myrmicinae						
Dacetini						
Daceton	Daceton armigerum	2,5-Dimethylpyrazine	Amine	C03	108,14	(Morgan et al., 1992)
		2,3,5-Trimethylpyrazine	Amine	C04	122,17	
		2,5-Dimethyl-3-ethylpyrazine	Amine	C05	136,19	
		9-Tricosene	Hydrocarbon	C23	324,63	
		Tricosane	Hydrocarbon	C23	324,63	
		9-Pentacosene	Hydrocarbon	C25	350,66	
Solenopsidini						
Monomorium	Monomorium pharaonis	3-Butyl-5-methyloctahydroindolizine	Amine	C13	195,34	(Edwards and Chambers, 1984; Ritter et al., 1977)
		monomorine I	Amine	C13	195,34	
		monomorine III	Amine	C15	223,4	
		faranal	carboxylic acid	C13	250,42	
		monomorine V	Amine	C14	267,49	
		monomorine I	Amine	C13	195,34	
		monomorine II	Amine	C13	197,36	
		monomorine III	Amine	C15	223,4	
		monomorine IV	Amine	C14	239,44	
Solenopsis	Solenopsis invicta	Z,E-alpha-farnesene	Hydrocarbon	C12	204,35	(Williams et al. 1981; Van der Meer et al. 1981, Van der Meer 1983; Van der Meer et al. 1988)
		E,E-alpha-farnesene	Hydrocarbon	C12	204,35	
		Z,E-alpha-homofarnesene	Hydrocarbon	C12	218,38	
		Z,Z-alpha-homofarnesene	Hydrocarbon	C12	218,38	
		Heptadecane	Hydrocarbon	C17	240,47	
		Z,Z,Z-allofarnesene	Hydrocarbon	C12	204,35	
Myemicini						
Eutetramorium	Eutetramorium mocquerysi	2,3-Dimethyl-5-(2-methylpropyl)-pyrazine	Amine	C05	164,25	(Tentschert et al., 2000)
Manica	Manica rubida	2,5-Dimethyl-3-ethylpyrazine	Amine	C05	136,19	(Attygalle et al., 1986)
Myrmica	Myrmica lobicornis	2,5-Dimethyl-3-ethylpyrazine	Amine	C05	136,19	(Evershed et al., 1981)
	Myrmica rubra	2,5-Dimethyl-3-ethylpyrazine	Amine	C05	136,19	(Evershed et al., 1981)
	Myrmica ruginodis	2,5-Dimethyl-3-ethylpyrazine	Amine	C05	136,19	(Evershed et al., 1981)
	Myrmica rugulosa	2,5-Dimethyl-3-ethylpyrazine	Amine	C05	136,19	(Evershed et al., 1981)
	Myrmica sabuleti	2,5-Dimethyl-3-ethylpyrazine	Amine	C05	136,19	(Evershed et al., 1981)
	Myrmica scabrinodis	2,5-Dimethyl-3-ethylpyrazine	Amine	C05	136,19	(Evershed et al., 1981)
	Myrmica schencki	2,5-Dimethyl-3-ethylpyrazine	Amine	C05	136,19	(Evershed et al., 1981)
	Myrmica suicinodis	2,5-Dimethyl-3-ethylpyrazine	Amine	C05	136,19	(Evershed et al., 1981)
Pogonomyrmex	Pogonomyrmex barbatus	2,3,5-Trimethylpyrazine	Amine	C04	122,17	(Hölldobler et al., 2001)
		2,5-Dimethyl-3-ethylpyrazine	Amine	C05	136,19	
		2,5-Dimethylpyrazine	Amine	C03	108,14	
	Pogonomyrmex maricopa	2,3,5-Trimethylpyrazine	Amine	C04	122,17	(Hölldobler et al., 2001)
		2,5-Dimethyl-3-ethylpyrazine	Amine	C05	136,19	
		2,5-Dimethylpyrazine	Amine	C03	108,14	
	Pogonomyrmex occidentalis	2,3,5-Trimethylpyrazine	Amine	C04	122,17	(Hölldobler et al., 2001)

— *continued from previous page*

GENUS	SPECIES	CHEMICAL COMPOUNDS	FUNCTIONAL GROUP	CHAIN LENGTH	MOLECULAR WEIGHT	REFERENCES
		2,5-Dimethyl-3-ethylpyrazine	Amine	C05	136,19	
		2,5-Dimethylpyrazine	Amine	C03	108,14	
	Pogonomyrmex rugosus	2,3,5-Trimethylpyrazine	Amine	C04	122,17	(Hölldobler et al., 2001)
		2,5-Dimethyl-3-ethylpyrazine	Amine	C05	136,19	
		2,5-Dimethylpyrazine	Amine	C03	108,14	
Tetramoriini						
Tetramorium	Tetramorium caespitum	2,5-Dimethylpyrazine	Amine	C03	108,14	(Attygalle and Morgan, 1983, 1984)
		2,5-Dimethyl-3-ethylpyrazine	Amine	C05	136,19	
	Tetramorium impurum	Methyl 2-hydroxy-6-methylbenzoate	Phenol	C08	166,17	(Morgan and Ollett, 1987; Morgan et al., 1990)
	Tetramorium meridionale	2-Methylpyrazine	Amine	C03	94,11	(Jackson et al., 1990)
		2,5-Dimethylpyrazine	Amine	C03	108,14	
		2,3,5-Trimethylpyrazine	Amine	C04	122,17	
		2,5-Dimethyl-3-ethylpyrazine	Amine	C05	136,19	
Pheidolini						
Aphaenogaster	Aphaenogaster albisetosus	(4S)-4-Methylheptan-3-one	Ketone	C07	128,21	(Hölldobler, 1995)
		(4R)-4-Methylheptan-3-one	Ketone	C07	128,21	
	Aphaenogaster cockerelli	(1R)-1-Phenylethanol	Alcool I	C08	122,16	(Hölldobler, 1995)
		(4S)-4-Methylheptan-3-one	Ketone	C07	128,21	
	Aphaenogaster rudis	anabasine	Amine	C09	162,23	(Attygalle et al., 1998a)
		anabaseine	Amine	C09	160,22	
		2-(Pyridin-3-yl)-pyridine	Amine	C09	156,18	
		N-Isopentyl-2-phenylethylamine	Amine	C08	191,31	
Messor	Messor bouvieri	anabasine	Amine	C09	162,23	(Jackson et al., 1989)
		2,5-Dimethyl-3-ethylpyrazine	Amine	C05	136,19	
	Messor capensis	anabasine	Amine	C09	162,23	(Brand and Mpuru, 1993)
		anabaseine	Amine	C09	160,22	
	Messor ebeninus	anabasine	Amine	C09	162,23	(Coll et al., 1987)
Pheidole	Pheidole pallidula	2,5-Dimethyl-3-ethylpyrazine	Amine	C05	136,19	(Ali et al., 1988)
Pristomyrmex	Pristomyrmex pungens	6-Pentyl-2H-pyran-2-one	Ketone	C10	166,22	(Janssen et al., 1997a)
Cermatogastrini						
Crematogaster	Crematogaster castanea	(R)-dodecan-2-ol	Alcool II	C12	186,33	(Morgan et al., 2004)
Attini						
Acromyrmex	Acromyrmex octopinosus	Methyl 4-methylpyrrole-2-carboxylate	Amine	C05	139,15	(Cross et al., 1982; Evershed and Morgan, 1983)
		Acetaldehyde	Aldehyde	C02	44,05	
		2,5-Dimethyl-3-ethylpyrazine	Amine	C05	136,19	
		3,5-Dimethyl-2-ethylpyrazine	Amine	C05	136,2	
	Acromyrmex subterraneus subterraneus	Methyl 4-methylpyrrole-2-carboxylate	Amine	C05	139,15	(Do Nascimento et al., 1994)
Atta	Atta bisphaerica	Methyl 4-methylpyrrole-2-carboxylate	Amine	C05	139,15	(De Oliveira et al., 1990)
		2,5-Dimethyl-3-ethylpyrazine	Amine	C05	136,19	
		2-Phenylacetic acid	Carboxylic acid	C08	136,15	
		bornylene	Hydrocarbon	C09	136,23	
		Octan-1-ol	Alcool I	C08	130,23	
	Atta cephalotes	Methyl 4-methylpyrrole-2-carboxylate	Amine	C05	139,15	(Riley et al., 1974; Evershed and Morgan, 1983)

— continued from previous page

GENUS	SPECIES	CHEMICAL COMPOUNDS	FUNCTIONAL GROUP	CHAIN LENGTH	MOLECULAR WEIGHT	REFERENCES
		2,5-Dimethyl-3-ethylpyrazine	Amine	C05	136,19	
		Acetaldehyde	Aldehyde	C02	44,05	
	Atta laevigata	Methyl 4-methylpyrrole-2-carboxylate	Amine	C05	139,15	(De Oliveira et al., 1990)
		2-Phenylacetic acid	Carboxylic acid	C08	136,15	
		bornylene	Hydrocarbon	C09	136,23	
		Octan-1-ol	Alcool I	C08	130,23	
	Atta sexdens	Methyl 4-methylpyrrole-2-carboxylate	Amine	C05	139,15	(Robinson and Cherrett, 1978)
	Atta sexdens rubropilosa	Methyl 4-methylpyrrole-2-carboxylate	Amine	C05	139,15	(Evershed and Morgan, 1983)
		2,5-Dimethyl-3-ethylpyrazine	Amine	C05	136,19	
		Acetaldehyde	Aldehyde	C02	44,05	
		2,5-Dimethyl-3-ethylpyrazine	Amine	C05	136,19	(Cross et al., 1979)
		Methyl 2-phenylacetate	Acetate ester	C08	164,2	
		Ethyl 2-phenylacetate	Acetate ester	C08	164,2	
		Methyl 4-methylpyrrole-2-carboxylate	Amine	C05	139,15	
	Atta sexdens sexdens	2,5-Dimethyl-3-ethylpyrazine	Amine	C05	136,19	(Evershed and Morgan 1983; Billen et al. 1992, Morgan et al. 2006)
		2,5-Dimethylpyrazine	Amine	C03	108,14	
		2,3,5-Trimethylpyrazine	Amine	C04	122,17	
		Methyl 4-methylpyrrole-2-carboxylate	Amine	C05	139,15	
		Acetaldehyde	Aldehyde	C02	44,05	
	Atta texana	Methyl 4-methylpyrrole-2-carboxylate	Amine	C05	139,15	(Tumlinson et al., 1972)
		Methyl 4-methylpyrrole-2-carboxylate	Amine	C05	139,15	(Sonnet and Moser, 1972)
Metoponini						
Metapone	Metapone madagascarica	Methyl pyrrole-2-carboxylate	Amine	C05	125,13	(Hölldobler et al., 2002)
no tribu						
Mayriella	Mayriella overbecki	Methyl 2-hydroxy-6-methylbenzoate	Phenol	C08	166,17	(Kohl et al., 2000)
Dolichoderinae						
Dolichoderini						
Dolichoderus	Dolichoderus thoracicus	(Z)-9-Octadecenal	Aldehyde	C18	266,47	(Attygalle et al., 1998b)
		(Z)-9-Hexadecenal	Aldehyde	C16	238,41	
Tapinomini						
Linepithema	Linepithema humile	(Z)-9-Hexadecenal	Aldehyde	C16	238,41	(Cavill et al., 1979; Van Vorhis Key and Baker, 1982)
Tapinoma	Tapinoma simrothi	Iridodial	Aldehyde	C07	154,21	(Simon and Hefetz, 1991)
		Iridomyrmecin	Ketone	C08	168,23	
Formicinae						
Lasiini						
Lasius	Lasius fuliginosus	mellein	Ketone	C10	178,19	(Huwyler et al. 1975; Akino and Yamaoka 1996, Kern et al. 1997)
		2,3-Dihydro-3,5-dihydroxy-6-methyl-4(H)-pyran-4-one	Ketone	C06	144,13	
		Hexanoic acid	Carboxylic acid	C06	116,16	
		Heptanoic acid	Carboxylic acid	C07	130,19	
		Octanoic acid	Carboxylic acid	C08	144,21	
		Nonanoic acid	Carboxylic acid	C09	158,24	
		Decanoic acid	Carboxylic acid	C10	172,26	

— *continued from previous page*

Genus	Species	Chemical compounds	Functional group	Chain Length	Molecular Weight	References
		Dodecanoic Acid	Carboxylic acid	C12	200,32	
	Lasius niger	3,4-Dihydro-8-hydroxy-3,5,7-trimethylisocoumarin	Ketone	C10	206,24	(Bestmann et al., 1992)
Camponotini						
Camponotus	Camponotus atriceps	6-sec-Butyl-tetrahydro-3,5-dimethylpyran-2-one	Pyran	C08	184,26	(Haak et al., 2001)
		geranic acid	Carboxylic acid	C08	168,23	
	Camponotus balzani	8-Hydroxy-3,5,7-trimethylisochroman-1-one	Ketone	C08	206,24	(Kohl et al., 2003)
	Camponotus castaneus	6-sec-Butyl-tetrahydro-3,5-dimethylpyran-2-one	Pyran	C08	184,26	(Kohl et al., 2003)
	Camponotus floridanus	6-sec-Butyl-tetrahydro-3,5-dimethylpyran-2-one	Pyran	C08	184,26	(Haak et al., 2001)
		geranic acid	Carboxylic acid	C08	168,23	
	Camponotus herculeanus	(2S,4R,5S)-2,4-Dimethyl-5-hexanolide	Cyclic ester	C06	142,2	(Bestmann et al., 1999)
	Camponotus ligniperda	(2S,4R,5S)-2,4-Dimethyl-5-hexanolide	Cyclic ester	C06	142,2	(Bestmann et al., 1999)
	Camponotus pennsylvanicus	(2S,4R,5S)-2,4-Dimethyl-5-hexanolide	Cyclic ester	C06	142,2	(Kohl et al., 2003)
	Camponotus rufipes	mellein	Ketone	C10	178,19	(Uebler et al., 1995)
	Camponotus sericeiventris	8-Hydroxy-3,5,7-trimethylisochroman-1-one	Ketone	C08	206,24	(Kohl et al., 2003)
	Camponotus silvicola	8-Hydroxy-3,5,7-trimethylisochroman-1-one	Ketone	C08	206,24	(Uebler et al., 1995)
	Camponotus socius	(2S,4R,5S)-2,4-Dimethyl-5-hexanolide	Cyclic ester	C06	142,2	(Bestmann et al., 1999; Kohl et al., 2001)
		2,3-Dihydro-3,5-dihydroxy-6-methyl-4(H)-pyran-4-one	Ketone	C06	144,13	
	Camponotus vagus	(2S,4R,5S)-2,4-Dimethyl-5-hexanolide	Cyclic ester	C06	142,2	(Bestmann et al., 1999)
Ponerinae						
Ectatommini						
Gnamptogenys	Gnamptogenys striatula	4-methylgeraniol	Alcool I	C08	168,28	(Blatrix et al., 2002)
		(E)-3,4,7-Trimethyl-2,6-nonadien-1-ol	Alcool I	C09	182,3	
		(E)-2,(4S)-3,4,7-Trimethyl-2,6-octadienyl decanoate	Carboxylic ester	C10	322,53	
		(E)-2,(4S),6-3,4,7-Trimethyl-2,6-octadienyl dodecanoate	Carboxylic ester	C12	350,58	
Ponerini						
Leptogenys	Leptogenys diminuta	(3R,4S)-4-Methylheptan-3-ol	Alcool II	C07	130,23	(Attygalle et al., 1988, 1991; Kern and Bestmann, 1993)
		isogeraniol	Alcool I	C08	154,25	
	Leptogenys peuqueti	1-Ethyl-4-methylheptyl acetate	Acetate ester	C08	200,32	(Janssen et al., 1997b)
		1-Isopropyl-4-methylheptyl acetate	Acetate ester	C08	214,34	
		1-Propyl-4-methylheptyl acetate	Acetate ester	C09	214,34	
		4-Methyldodecan-7-ol	Alcool II	C11	200,36	
		3,9-Dimethyldodecan-6-ol	Alcool II	C12	214,39	
		1-Pentyl-4-methylheptyl acetate	Acetate ester	C11	242,4	
		4-Methyltridecan-7-ol	Alcool II	C13	214,39	
		4-Methyltetradecan-7-ol	Alcool II	C14	228,41	
		4,10-Dimethyltridecan-7-ol	Alcool II	C13	228,41	
		1-(3-Methylhexyl)-4-methylheptyl acetate	Acetate ester	C13	270,45	
		1-(3-Methylhexyl)-octyl acetate	Acetate ester	C14	270,45	
		1-Heptyloctyl acetate	Acetate ester	C15	270,45	
		4-Methylhexadecan-7-ol	Alcool II	C16	256,47	
		1-(3-Methylhexyl)-decyl acetate	Acetate ester	C16	298,5	
Megaponera	Megaponera foetens	N,N-Dimethyluracil	Amine	C03	140,14	(Longhurst et al., 1979; Janssen et al., 1995)
		actinidine	Amine	C08	147,22	

— continued from previous page

GENUS	SPECIES	CHEMICAL COMPOUNDS	FUNCTIONAL GROUP	CHAIN LENGTH	MOLECULAR WEIGHT	REFERENCES
		1,2-Dimethyldisulfate	Sulphur compound	C01	94,2	
		1,3-Dimethyltrisulfate	Sulphur compound	C01	126,26	
		Benzyl methyl sulfane	Sulphur compound	C07	138,23	
Pachycondyla	Pachycondyla tarsata	Heptadecan-9-one	Ketone	C17	254,45	(Janssen et al., 1999)
Ectatomminae						
Ectatommini						
Ectatomma	Ectatomma ruidum	geranylgeraniol acetate	Acetate ester	C16	332,52	(Bestmann et al., 1995)
		geranylgeraniol	Alcool I	C16	290,48	
Rhytidoponera	Rhytidoponera metallica	isogeraniol	Alcool I	C08	154,25	(Meinwald et al., 1983)
		3-Hydroxybenzaldehyde	Aldehyde	C06	122,12	
Dorylinae						
Aenictini						
Aenictus	Aenictus sp	Methyl 2-aminobenzoate	Carboxylic ester	C07	151,16	(Oldham et al., 1994)
		Methyl 3-pyridinecarboxylate	Amine	C05	137,14	

Summary

A fundamental challenge in Community Ecology is to understand the mechanisms allowing species coexistence. In ant communities, the structuring role of inter-specific competition is essential. Some behaviourally dominant species displace behaviourally subordinate species at food resources. The coexistence between dominant and subordinate species is mediated by competitive trade-offs. In Mediterranean ant communities, species' competitive abilities are linked to their foraging strategies. More dominant species generally display higher degree of communication when foraging. This dissertation investigates how foraging strategies underpin competitive trade-offs and structure ant communities.

The first part focuses on the part played by foraging strategies in the alternative between finding food fast or being able to drive competitors away. This Dominance-Discovery trade-off is underlain by the allocation of colony workers between those who seek for resources, and those who exploit and defend them. The mathematical models proposed are developed at the evolutionary timescale and demonstrate that this simple principle might explain foraging strategy diversification. The theoretical structure suggested might be broadened and used as a framework to study life history traits evolutionary dynamics in eusocial insects.

The second part is centred on the Dominance-Thermal Tolerance trade-off. Dominant species are usually more sensitive to stressful temperatures, i.e. high temperature in Mediterranean communities. The underlying hypothesis deals with the pheromone function in ant communication. Since chemical compounds are deteriorated at high temperatures, the benefit of using foraging strategies based of chemical communication might be moderated. In Mediterranean ecosystems submitted to important seasonal and daily temperature variations, foraging strategy diversity contribute thereby to ant communities diversity.