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Statistics and dynamics of interaction networks and division of labor in ants

Braunschweig Raphaël

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Département d'écologie et évolution

Statistics and dynamics of interaction networks and division of labor in ants

Thèse de doctorat ès sciences de la vie (PhD)

présentée à la
Faculté de biologie et de médecine
de l'Université de Lausanne

par

Raphaël BRAUNSCHWEIG

Titulaire d'un Master of Science MSc en Physique de l'EPFL, Suisse

Jury

Prof. Olivier Michielin (Institut suisse de bioinformatique, UNIL), Président
Prof. Laurent Keller (Département d'écologie et évolution, UNIL), Directeur de thèse
Prof. Paolo De Los Rios (Institut de physique, EPFL), Co-directeur de thèse
Dre Yuko Ulrich (Département d'écologie et évolution, UNIL), experte
Dr Ofer Feinerman (Department of physics of complex systems, Weizmann Institute of Science), expert

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Co-directeur·trice	Monsieur Prof. Paolo **De Los Rios**
Expert·e·s	Madame Dre Yuko **Ulrich**
	Monsieur Dr Ofer **Feinerman**

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Statistics and Dynamics of Interaction Networks and Division of Labor in Ants

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pour le Doyen
de la Faculté de biologie et de médecine

Prof. Olivier Michielin

Summary

Division of labor, which contributed to the ecological success of ants, does not arise from centralized control, but is an emergent, self-organized phenomenon which is believed to be at least partially mediated through social interactions. However, how social interactions contribute to division of labor is still poorly understood. Workers change tasks throughout their life, in general from nursing to foraging, but a precise individual-level quantification and prediction of the task *dynamics* (i.e. change) and the related social dynamics is still missing.

In Chapter 1, we analyzed colony-wide interaction networks of six unperturbed colonies of the ant *Camponotus fellah* tracked during 11 days. This analysis revealed that each network consists of two overlapping groups: the nurse social group comprising nurses and the queen, and the forager social group. We show that the social network is a continuum on which ants gradually move from the nurse to the forager social group. To quantify this group change, we estimated the *social maturity* — to what extent an individual belonged to the forager group — for each ant and on each day. We show that, for each colony, the long-term social dynamics of each individual worker of the colony can be mapped to a single colony-specific sigmoidal curve. This curve predicts future individual behavioral changes of a worker significantly better than models assuming a linear change or no change at all. Such slow-fast-slow sigmoidal dynamics are typical of regulatory mechanisms.

In Chapter 2, we then asked how the social maturity of a worker was related to its *task specialization* which we calculated by measuring the number of visits of the worker to the foraging arena and the number of visits of the worker to the brood pile. The task specialization and the social maturity of individual ants in each colony were positively correlated. However, despite all colonies following the expected nurse to forager task dynamics, two colonies followed the inverse social dynamics from the forager social group to the nurse social group. This discrepancy between the task and the social dynamics, which are both individual-level properties, could be explained by a colony-level (relatively) static property: the distance between nest entrance and brood pile which was positively correlated with the expected maximum social maturation rate. We then studied how another colony-level property — the spatial segregation of the ants — is related to task and social dynamics. Using a machine-learning algorithm, we showed that individuals could be classified according to three *spatial segregation zones* (SSZs): the nursing SSZ, the foraging SSZ and the intermediate SSZ. Further, for most colonies, the overlap between the foraging and the nursing SSZs was lower than the overlaps of both SSZs with the intermediate SSZ. Therefore, the intermediate SSZ links the two other SSZs. Furthermore, when intermediate workers used the two other SSZs equally (i.e. in a balanced way), transitions from nursing to foraging were faster, highlighting the importance of the intermediate SSZ as a (balanced) link between the nursing and the foraging SSZs for regulating task dynamics. Finally, task transitions from nursing to foraging were faster when the three SSZs overlapped less, highlighting that spatial segregation, by increasing stimulus perception, accelerates task transitions, which in turn could enhance efficiency. Overall, our results highlight the link between individual-level dynamic properties (here, task and social dynamics) and colony-level structures (here, the entrance-brood distance and the spatial segregation of the ants), therefore revealing parts of the workings of self-organization.

Chapter 1 and 2 focused on the social maturation and task specialization of workers of an unperturbed colony. However, ant colonies are often exposed to external perturbations that can damage them. To overcome this damage, ant colonies are believed to show flexibility and resilience. However, evidence that ant colonies can flexibly adjust to perturbations through behavioral changes of workers is still controversial and varies from ant species to ant species.

In Chapter 3, to investigate the resilience of *C. fellah* ant colonies to the loss of some specific group of workers, we performed an experiment where we first tracked all ants in 15 colonies over a week. We then selectively removed workers from each colony. We removed the 25% of workers most embedded in the forager social group (i.e. with the highest social maturity) in a first treatment, the 25% of workers most embedded in the nurse social group (i.e. with the lowest social maturity) in a second treatment, and 25% of workers uniformly distributed in the social maturity scale to act as a control. Surprisingly, subsequent tracking of these colonies for another two weeks revealed that the remaining workers do not compensate for the lost workforce. Workers pursued their normal task specialization time line independently of treatment suggesting that the task specialization time line of *C. fellah* is rigidly preprogramed rather than flexibly adjusting in response to perturbations. In addition, we found that the ants do not perform any active change of their social interactions (i.e. *no active rewiring*) to change the social group structure in response to the removal. Therefore, it seems that, in terms of social group structure, *C. fellah* stays passive in response to the removal. Finally, six days or more after the forager removal, the number of interaction partners and the number of interactions per ants decreased, compared to a "no active rewiring" null hypothesis, significantly more than in the nurse removal and the control. The removal of the foragers therefore led to the highest disturbance of the network connectivity, highlighting the key contribution of the foragers to the network overall connectivity.

Résumé

La division du travail, qui a contribué au succès écologique des fourmis, ne survient pas d'un contrôle centralisé, mais est un phénomène émergent et auto-organisé que l'on croit être au moins partiellement régulé par les interactions sociales. Cependant, la manière dont les interactions sociales contribuent à la division du travail est encore peu comprise. Les ouvrières changent de tâches tout au long de leur vie, en général, commençant par être *nourrices* (qui s'occupent du couvain et de la reine) et finissant par être *fourrageuses* (qui s'occupent de la recherche de nourriture), mais une quantification et une prédiction précise et individuelle de la *dynamique* (c.-à-d. du changement) de tâche et de la dynamique sociale n'ont pas encore été entreprises.

Dans le chapitre 1, nous avons analysé les réseaux d'interactions sociales de six colonies de *Camponotus fellah* dont tous les individus ont été suivis pendant 11 jours. Cette analyse a révélé que chaque réseau se compose de deux groupes qui se chevauchent: le groupe social des nourrices comprenant les nourrices et la reine, et le groupe social des fourrageuses. Nous montrons que le réseau social est un continuum sur lequel les fourmis se déplacent graduellement du groupe social des nourrices à celui des fourrageuses. Pour quantifier ce changement de groupe, nous avons estimé la *maturité sociale* — dans quelle mesure un individu appartenait au groupe des fourrageuses — pour chaque fourmi et chaque jour. Nous montrons que, pour chaque colonie, la dynamique sociale à long terme de chaque ouvrière de la colonie peut être associée à une seule courbe sigmoïdale spécifique à la colonie. Cette courbe prédit les changements comportementaux individuels futurs d'une ouvrière significativement mieux que des modèles supposant un changement linéaire ou pas de changement du tout. Une telle dynamique sigmoïdale (lent-rapide-lent) est typique des mécanismes de régulations.

Dans le chapitre 2, nous avons ensuite investigué comment la maturité sociale d'une ouvrière était liée à sa *spécialisation de tâche* que nous avons calculée en mesurant le nombre de sorties du nid de l'ouvrière et son nombre de visites à la pile de couvain. La spécialisation de tâche et la maturité sociale des fourmis individuelles dans chaque colonie étaient positivement corrélées. Cependant, bien que toutes les colonies suivissent la dynamique de tâche attendue, c.-à-d. de nourrice à fourrageuse, deux colonies suivaient la dynamique sociale inverse, du groupe social des fourrageuses à celui des nourrices. Cette différence entre la dynamique de tâche et la dynamique sociale, qui sont toutes deux des propriétés individuelles, pourrait s'expliquer par une propriété (relativement) statique au niveau de la colonie: la distance entre l'entrée du nid et la pile de couvain qui était positivement corrélée avec le taux de maturation social. Nous avons ensuite étudié comment une autre propriété au niveau des colonies — la ségrégation spatiale des fourmis — est liée à la dynamique de tâche et la dynamique sociale. En utilisant un algorithme d'apprentissage automatique (*machine learning*), nous avons montré que les individus pouvaient être classés selon trois *zones de ségrégation spatiale* (ZSS): la ZSS du soin au couvain, la ZSS de fourragement et la ZSS intermédiaire. De plus, pour la majorité des colonies, le chevauchement entre la ZSS de fourragement et la ZSS du soin au couvain était inférieur aux chevauchements de chacune des deux ZSS avec la ZSS intermédiaire. Donc, la ZSS intermédiaire lie les deux autres ZSS. De plus, lorsque les ouvrières intermédiaires utilisaient les deux autres ZSS de manière égales (c.-à-d. de manière équilibrée), les transitions depuis le soin au couvain vers la recherche de nourriture étaient plus rapides, soulignant l'importance de la ZSS intermédiaire comme lien (équilibré) entre ZSS du soin au couvain et la ZSS de fourragement pour la régulation de la dynamique de tâche. Enfin, les transitions de tâche des soins au couvain à la recherche de nourriture étaient plus rapides lorsque les trois ZSS se chevauchaient moins, soulignant que la ségrégation spatiale, en augmentant la perception des stimuli, accélère les transitions de tâches, ce qui pourrait améliorer l'efficacité de la colonie. Dans l'ensemble, nos résultats mettent en évidence le lien entre les propriétés dynamiques individuelles (ici, dynamique de tâches et sociale) et les structures au niveau de la colonie (ici, la distance couvain-entrée et la ségrégation spatiale des fourmis), et de ce fait révèlent une partie du fonctionnement de l'auto-organisation.

Les chapitres 1 et 2 étaient focalisés sur la maturation sociale et la spécialisation de tâche des ouvrières de colonies non perturbées. Cependant, les colonies de fourmis sont souvent exposées à des perturbations externes qui peuvent les endommager. On s'accorde généralement sur le fait que, pour surmonter ces dommages, les colonies de fourmis font preuve de flexibilité et de résilience. Cependant, les preuves expérimentales que les colonies de fourmis peuvent s'adapter avec flexibilité à des perturbations par des changements comportementaux des ouvrières sont encore controversées et varient d'une espèce de fourmi à l'autre.

Dans le chapitre 3, pour étudier la résilience des colonies de la fourmi *C. fellah* à la perte d'un groupe spécifique d'ouvrières, nous avons effectué une expérience où nous avons d'abord suivi toutes les fourmis dans 15 colonies sur une semaine. Nous avons ensuite retiré sélectivement des ouvrières de chaque colonie. Nous avons retiré les 25% des ouvrières les plus intégrées dans le groupe social des fourrageuses (c.-à-d. avec les maturités sociales les plus élevés) dans un premier traitement, les 25% des ouvrières les plus intégrées dans le groupe social des nourrices (c.-à-d. avec les maturités sociales les plus faibles) dans un deuxième traitement, et 25% des ouvrières uniformément distribuées sur l'échelle de maturité sociale en tant que contrôle. Étonnamment, un suivi ultérieur de ces colonies pendant deux semaines a révélé que les ouvrières restantes ne remplacent pas les ouvrières perdues. Les ouvrières ont poursuivi leur trajectoire habituelle de spécialisation de tâche indépendamment du traitement, ce qui suggère que leur trajectoire de spécialisation de tâche est préprogrammée de façon rigide plutôt que s'ajustant avec flexibilité aux perturbations. En outre, nous avons constaté que les fourmis n'effectuent pas de changement actif de leurs interactions sociales (c.-à-d. *pas de recâblage actif* de leur réseau social) pour changer la structure des groupes sociaux en réponse à la perte des ouvrières. Par conséquent, il semble que, en termes de structure des groupes sociaux, *C. fellah* reste passif en réponse à la perte de ses ouvrières. Enfin, six jours ou plus après le retrait des fourrageuses, le nombre de partenaires d'interactions et le nombre d'interactions par fourmis ont diminué, par rapport à une hypothèse nulle supposant «'pas de recâblage actif»', significativement plus que dans le retrait des nourrices et le contrôle. Le retrait des fourrageuses a donc conduit à la perturbation la plus élevée de la connectivité du réseau, mettant en évidence la contribution clé des fourrageuses à la connectivité globale du réseau.

Résumé grand publique

Titre de la thèse en français: *Statistique et dynamique des réseaux d'interactions et de la division du travail chez les fourmis*

Les fourmis sont partout et extrêmement nombreuses ! En effet, il y a des espèces de fourmis indigènes à toutes les régions terrestres sauf l'Antarctique, le Groenland, l'Islande et quelques petites îles et le poids de toutes les fourmis de la terre combinées correspond au poids de tous les êtres humains, bien qu'une fourmi soit environ 21 million de fois plus légère qu'un être humain ! On parle ici du *succès écologique* des fourmis. Une des raisons principales de ce succès écologique est leur division du travail. Cette division du travail ne survient pas d'un contrôle centralisé, mais est un phénomène auto-organisé que l'on croit être au moins partiellement régi par les interactions sociales. Toutefois, la manière dont les interactions sociales contribuent à la division du travail est encore peu comprise. De plus, les ouvrières changent de tâches tout au long de leur vie, en général, commençant par le rôle de *nourrices* qui s'occupent du *couvain* (entre autres, œufs et larves) et de la reine, et finissant par le rôle de *fourrageuses* qui s'occupent de la recherche de nourriture. Cependant, une quantification et une prédiction précise et individuelle du changement de tâche et des interactions sociales n'ont pas encore été entreprises.

Dans le chapitre 1, nous avons analysé les réseaux d'interactions sociales de six colonies de la fourmi *Camponotus fellah* dont tous les individus ont été suivis pendant 11 jours. Cette analyse a révélé que chaque réseau se compose de deux groupes sociaux : le groupe social des nourrices comprenant les nourrices et la reine, et le groupe social des fourrageuses. De plus, nous montrons que ces deux groupes se *chevauchent*, c'est-à-dire que certaines fourmis appartiennent à la fois au groupe social des nourrices et à celui des fourrageuses. Nous montrons que les fourmis se déplacent graduellement sur ce réseau social : du groupe social des nourrices à celui des fourrageuses. Nous montrons également que ce mouvement est prévisible : les nourrices commencent par interagir un tout petit peu avec les fourrageuses et augmentent lentement leur nombre d'interactions avec les fourrageuses, puis ces fourmis interagissent de plus en plus et de plus en plus vite avec les fourrageuses, jusqu'à ce qu'elles se trouvent bien intégrées dans le groupe social des fourrageuses et qu'elles ralentissent à nouveau leur augmentation. Grâce à une formule mathématique qui décrit ce mouvement, nous avons pu prédire les interactions sociales futures de chacune des fourmis de nos colonies.

Dans le chapitre 2, nous avons ensuite analysé comment les interactions sociales d'une fourmi étaient liées à sa tâche. On a tout d'abord observé que plus la fourmi interagissait avec les nourrices, plus celle-ci s'occupait du couvain et que plus la fourmi interagissait avec les fourrageuses, plus celle-ci sortait du nid pour chercher de la nourriture. Nous avons ensuite étudié comment le changement de tâches et le changement de groupes sociaux des individus sont liés à des propriétés globales des colonies, comme la distance entre la pile de couvain et l'entrée du nid. Nous avons observé que plus la pile de couvain était proche de l'entrée du nid, plus le changement du groupe social des nourrices vers celui des fourrageuses était ralenti. Nous avons aussi montré que les fourmis se regroupaient dans trois différentes zones : une zone autour de la pile de couvain, une zone de fourragement et une zone intermédiaire qui sert de lien entre les deux premières zones. C'est lorsque les ouvrières qui étaient sur la zone intermédiaire utilisaient les deux autres zones de manière égale que les changements de tâches se faisaient le plus rapidement. Et c'est aussi lorsque les trois zones étaient le plus séparées que les changements de tâches se faisaient le plus rapidement. Dans l'ensemble, nos résultats mettent en évidence le lien entre les changements individuels (ici, changement de tâches et changement des interactions sociales) et la colonie vue globalement (ici, en regardant la distance entre le couvain et l'entrée du nid ou les différentes zones de regroupement des fourmis), et de ce fait révèlent une partie de l'(auto-)organisation d'une colonie de fourmis.

Les chapitres 1 et 2 étaient focalisés sur le changement de tâches et le changement de groupes sociaux des ouvrières de colonies non perturbées. Cependant, les colonies de fourmis sont souvent exposées à des perturbations externes qui peuvent les endommager. On s'accorde généralement sur le fait que, pour surmonter ces dommages, les colonies de fourmis font preuve de flexibilité et de résistance. Cependant, les preuves expérimentales que les colonies de fourmis peuvent s'adapter avec flexibilité à des perturbations par des changements du comportement des ouvrières sont encore controversées et varient d'une espèce de fourmi à l'autre.

Dans le chapitre 3, pour étudier la résistance des colonies de la fourmi *C. fellah* à la perte d'un groupe spécifique d'ouvrières, nous avons effectué une expérience où nous avons d'abord suivi toutes les fourmis dans 15 colonies sur une semaine. Nous avons ensuite retiré sélectivement des ouvrières de chaque colonie. Dans cinq colonies, nous avons retiré des nourrices. Dans cinq autres colonies, nous avons retiré des fourrageuses. Et dans les cinq dernières colonies, nous avons retiré un mélange de nourrices et de fourrageuses. Étonnamment, un suivi ultérieur de ces colonies pendant deux semaines a révélé que les ouvrières restantes ne remplacent pas les ouvrières perdues, ce qui suggère que leur changement de tâche est prédéterminé.

Contents

Chapter 1

Social group dynamics in ants

Collaborators on this chapter:

Raphaël Braunschweig; Danielle Mersch; Alessandro Crespi; Paolo De Los Rios; Laurent Keller

1.1 Introduction

Many animals display collective adaptive behaviors (Sumpter, 2006). Two striking examples are humans and ants. Both are ecologically highly successful, as each composes as much as 10% of the Earth's animal biomass and can be found on most terrestrial places on the globe (Hölldobler and Wilson, 1990). In both cases, this ecological success has been made possible through the evolution of complex social behavior and efficient division of labor. In ants, this division of labor does not arise from centralized control, but is an emergent, self-organized phenomenon (Bonabeau et al., 1997; Duarte et al., 2011; Wilson and Hölldobler, 1988) which is believed to be at least partially mediated through social interactions (Fewell, 2003; Mersch, 2016; O'Donnell and Bulova, 2007b; Robinson, 1992). This division of labor is also dynamic because workers change tasks as they age, in general from nursing to foraging (Hölldobler and Wilson, 1990;

Lenoir, 1979; Mersch et al., 2013b; Robinson, 1992; Seeley, 1982; Wilson, 1976). To get a complete picture of this dynamics of division of labor and the related dynamics of social interactions in ants requires to track all social interactions and task performances of an entire ant colony. Such tracking was first achieved in Mersch et al. (2013b). To explore whether the signature of division of labor — worker task performance — could be detected in the structure of the colony-wide interaction network in *Camponotus fellah*, the authors searched for the presence of *social groups* defined as a distinct subset of ants interacting more with each other than with ants in other social groups. Three social groups were detected, two of which were robust groups to which the same set of workers was affiliated on almost every day and contained together approximately two third of the workers. The first robust group, hereafter referred to as the *nurse group*, comprised the queen and workers who perform most visits to the brood. The second robust group, hereafter referred to as the *forager group*, comprised workers who perform most of the foraging trips. Therefore, workers specialized in nursing preferentially associated with other nurses and workers specialized in foraging preferentially associate with other foragers. The third social group, hereafter referred to as the *cleaner group*, comprised workers shown to perform most of the visits to the rubbish pile. This social group had less marked within-group preferential interactions than the two other social groups and occupied an intermediary position (within the network) between the two other groups (i.e. with workers of this group interacting with both nurses and foragers but nurses and foragers mostly not interacting directly with each other), suggesting that the cleaner group could belong to a continuum between the nurse and forager group. A social group structure with such a continuum between groups is called an *overlapping social group structure* (Fortunato, 2010; Lancichinetti et al., 2011; Lin et al., 2009). The approach of Mersch et al. (2013b) could not detect such overlapping social group structure and provide information on the day-to-day social group transition dynamics. However, detecting such overlapping social group structure and providing information on the day-to-day social group transition dynamics of all workers of the colony would be essential for understanding division of labor and temporal polyethism.

In this chapter, we dissect the overlapping group structure of the social network of unperturbed ant colonies. We then aim to mathematically describe and predict each worker's transition from one social group to the next on a long-term time scale. We reanalyzed the dataset of Mersch et al. (2013b), consisting of the daily social network of six unperturbed colonies of *C. fellah* during 11 days. We used recent tools (Fortunato, 2010; Lancichinetti et al., 2011; Lin et al., 2009) to detect whether an overlapping group structure is present in those social networks, to determine the number of groups and to quantify the group membership of each ant on each of the daily social networks. Finally, to mathematically describe and predict the long-term change of social group membership of workers — also referred to as *social maturation* — we created a predictive model of individual social maturation. We split the 11-day data into two datasets. The first seven days were used as a *training dataset* to fit the predictive model of individual social maturation, and the following four days were used as *validation dataset* to test the predictions of the model.

1.2 Results

To investigate whether an overlapping social group structure describes our daily ant social networks better than a non-overlapping social group structure, we ran the OSLOM social group detection algorithm (Lancichinetti et al., 2011). OLSOM detected an overlapping group structure (Fig. 1.1). With OSLOM, the overlap is not imposed, it is simply allowed. For this reason, our analysis showed that an overlapping social group structure describes our daily ant social networks better than a non-overlapping social group structure. In addition, OSLOM showed that, in 95% of the days (average across the six colonies), the daily interaction networks consisted of two overlapping groups (Fig. 1.1). Because OSLOM cannot assign group membership percentages, we then used the FacetNet social group detection algorithm (Lin et al., 2009). To detect the number of groups in the network with FacetNet, we ran FacetNet with a range of reasonable number of groups (1 to 10) and calculated the *soft modularity*. The *soft modularity* measures the strength of the subdivision of the network into groups (Lin et al., 2009) by calculating the deviation between the probability for within group interactions to be generated due to the group structure and the chance for interactions to be generated randomly. In each of the six colonies, we reached the strongest subdivision (i.e. maximum soft modularity) of the network over all 11 experimental days when networks were divided into two overlapping groups (Fig. 1.2a). We additionally verified whether this partitioning into two overlapping groups of the networks was optimal in each daily network (Fig. 1.2b). In 91% of the days (average across the six colonies), the optimal number of overlapping groups was two, suggesting that the number of identified social groups remained constant during the 11 days, which facilitates our subsequent analysis.

The group assignments obtained with FacetNet qualitatively match those shown previously (Mersch et al., 2013b) with one crucial difference (Fig. 1.3). Individuals previously assigned to the cleaner group are now classified as belonging to an overlap between the nurse and forager groups. Mersch et al. (2013b)'s nurses had an average social maturity (see Materials and methods section 1.5.2 for a detailed definition) of 0.09 and Mersch et al. (2013b)'s foragers had an average social maturity of 0.91, which means, consistently with Mersch et al. (2013b), that both nurses and foragers are well embedded in their respective groups. In contrast, for ants that were previously classified as cleaners we obtained group membership scores of 0.54 on average, suggesting that these individuals belong equally to both groups.

Importantly, FacetNet allowed us to identify ants that change their continuous social group membership (social maturity, see Materials and methods section 1.5.2) from one day to the next. By applying FacetNet to a sequence of daily interaction networks, we obtained for each ant i a time series of its social maturity, $S(i,t)$ which allowed us to build a predictive model tracing the social maturation of each individual as they transition from one social group to the other. We started by quantifying the change of social maturity over time for each ant. To achieve this, we performed a least-squares linear regression of the social maturity $S(i,t)$ on the training dataset (Fig. 1.4).

For each ant, the slope of the linear regression of the social maturity is an estimation of the rate of social maturation. Plotting this slope for each ant with respect to its average social maturity over the first seven days (training dataset), revealed that the social dynamics of a colony approximately follows a *hill function*, which is positive or negative depending on colonies (Fig. 1.5). For each colony, the hill function has a slope zero at $S(i,t) = 0$ or 1 and reaches maximum (resp. minimum) value at $S(i,t) = 0.5$. This hill function links the slope $m(i)$, or time-derivative dS/dt, of the social maturity to the social maturity S itself into a single differential equation, with a single colony-level parameter m_{max}. For a given colony, the parameter m_{max} corresponds to the expected maximum (resp. minimum) social maturation rate of a worker of this colony. For simplicity, we will henceforth refer to m_{max} as the *expected maximum social maturation rate* of a colony. The sign of m_{max} will tell us if it is a maximum ($m_{max} > 0$) or a minimum ($m_{max} < 0$). This differential equation is:

$$\frac{dS}{dt} = 4m_{max}(1-S)S. \tag{1.1}$$

The solution $S = S(t)$ of this differential equation is a sigmoidal curve. One of its possible parameterization is the following:

$$S = \frac{\tanh(2m_{max}t) + 1}{2}. \tag{1.2}$$

To obtain the long-term social maturation dynamics of a typical ant of the colony, we assume that all workers of a given colony undergo the same social maturation dynamics. To account for individual variation in the age at which behavioral transition occurs (Mersch et al., 2013b), our model does not require ants to start their social maturation at the same age. The sigmoidal solution (1.2) of the differential equation then represents the long-term social maturation dynamics of a typical ant of the colony (red curves on Fig. 1.6). This sigmoidal curve, also referred to as the maturation curve (because it refers to the social maturation of workers), is uniquely characterized by the parameter m_{max} obtained from the fit of the hill function. This fit was done with a non-linear least-squares model fit using the 'nls' function of the 'stats' library in 'R'. We then used the 'summary.nls' function of the same library to extract the estimated value of m_{max}, its standard error, t-statistic and corresponding (two-sided) p-value. The parameter m_{max} is the expected maximum social maturation rate of a worker of the colony, and as such summarizes the observed social dynamics of all workers of the colony into one single number. If a colony has $m_{max} > 0$, the sigmoidal model predicts, for a given worker of the colony, an increase of social maturity over time and therefore the expected transition from the nurse to the forager social group. Conversely, if a colony has $m_{max} < 0$, the sigmoidal model predicts, for a given worker of the colony, a decrease of social maturity over time and therefore an inverse transition, from the forager to the nurse social group.

Using our sigmoidal model, we found a significant sigmoidal trend, i.e. a significant m_{max} ($P < 0.05$), for five out of six colonies (Fig. 1.5 and Table 1.1). Four out of those five colonies exhibited the expected nurse to forager social transition (i.e. $m_{max} > 0$). However, the social dynamics of one colony (colony 58) was inverted (i.e. $m_{max} < 0$) and exhibited a forager to nurse social transition. To quantify the variation between ants in each colony, we computed the coefficient of determination R^2 that measures the proportion of the variance in the y-axis that is explained by the hill function (Fig. 1.5). The mean R^2 across all colonies was 0.154 ± 0.187, highlighting that a high proportion of the inter-individual variance is due to noise, which is characteristic of behavioral data.

To infer the *full social transition time* (t_{FT}) for each colony, we used the expected maximum social maturation rate m_{max} (see Materials and methods section 1.5.3). If $m_{max} > 0$, the full social transition time represents the time (in days) it would take an ant to transition fully from the nurse to the forager social group. If $m_{max} < 0$, the full social transition time is the time to transition from the forager to the nurse social group. Because of the high inter-colony variation in the magnitude of m_{max}, the full social transition time varied highly between colonies, with values ranging from 100 to 427 days for the four colonies with m_{max} significantly positive, a lower value of 63 days for the only colony with m_{max} significantly negative (colony 58) and a value of 612 days for the only colony with nonsignificant m_{max} (colony 78; Table 1.1).

We used the sigmoidal model fitted on the training dataset to predict future social maturity values for each ant. To test the predictive power of the sigmoidal model, we compared it to the predictive power of four alternative models that either assumed a linear change or no change at all. Each alternative model predicts social maturity using a different method. The first model uses the colony average. The second model uses each ant's average. The third model uses a line with the same slope for all ants of the colony. Finally, the fourth model, uses a linear regression for each ant. For more details on all this method, the statistical tests and the four alternative models, see Materials and methods section 1.5.4.

To illustrate the fit quality of the sigmoidal model predictions compared the observed values, we overlaid the whole sigmoidal curve model and the observed value of the validation dataset (days 8–11) for all ants of each colony (Fig. 1.6), which visually showed a good fit. This good fit was confirmed by the results of the statistical tests that showed that the sigmoid model predicted the future values of the social maturity significantly better ($P < 10^{-4}$) than all four alternative models (Table 1.2).

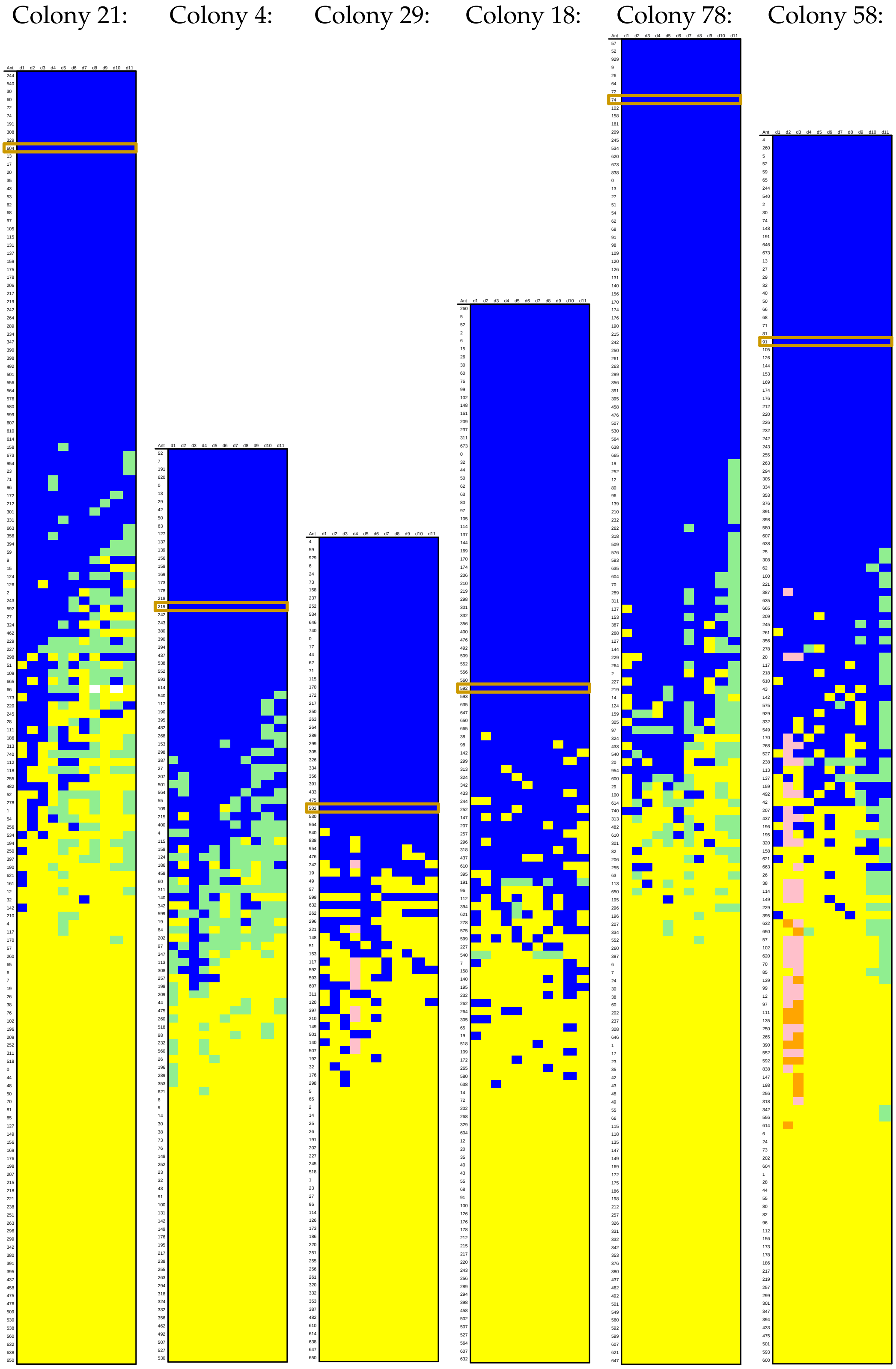

FIGURE 1.1: **Overlapping social group structure of two groups detected with OSLOM**. Each column is for a different colony. For each column: x-axis: time [day], y-axis: ants. Group colors: blue for nurses, yellow for foragers, green for the overlap between nurses and foragers, pink for the 3^{rd}group, orange for the overlap between the 3^{rd}group and the foragers. The queen is surrounded by a brown rectangle.

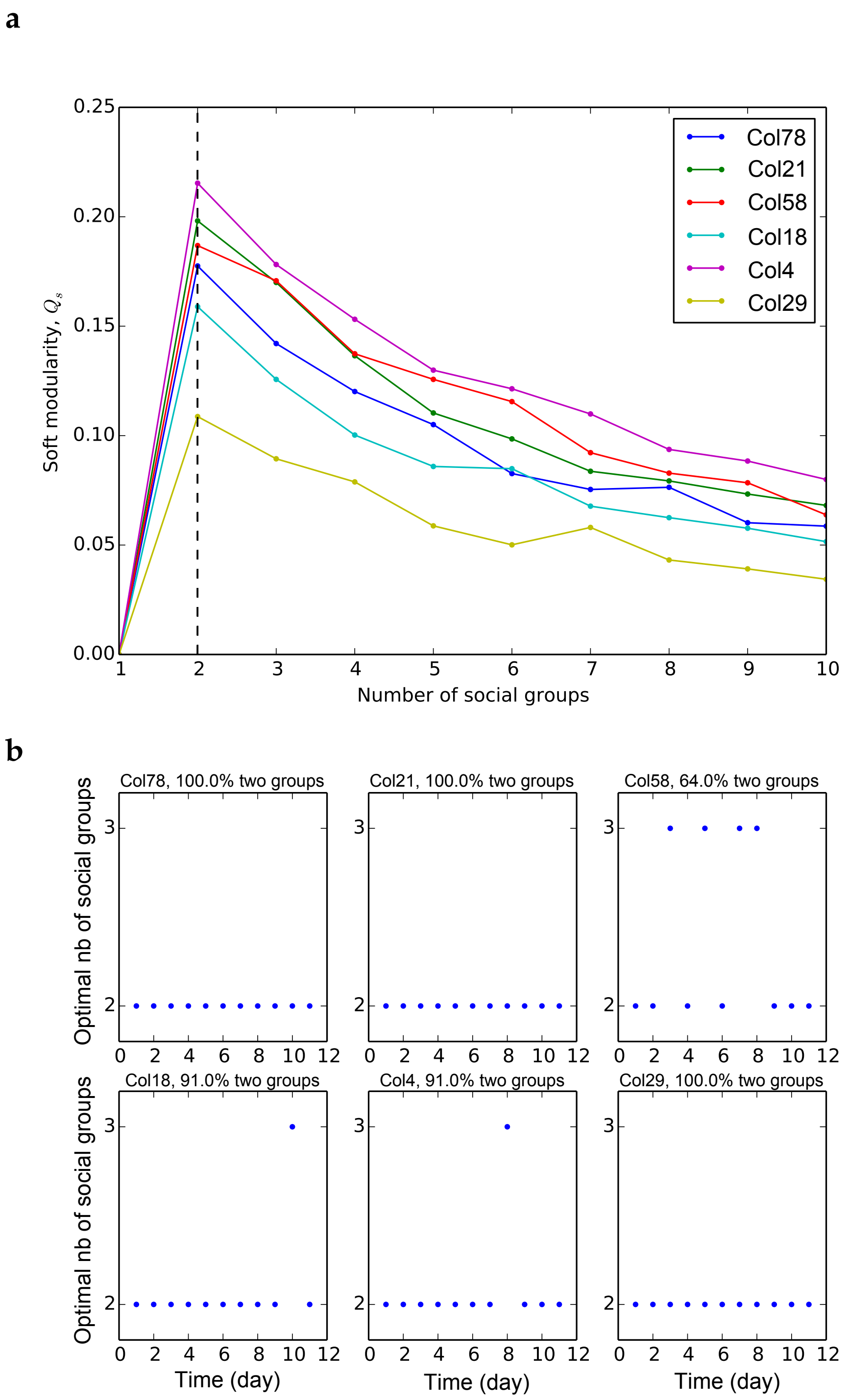

FIGURE 1.2: **Number of overlapping social groups identified by FacetNet (Lin et al., 2009)**. (**a**): Soft modularity (single number for a given network that measures the strength of the subdivision of the network into the different detected groups; Lin et al., 2009) as a function of the number of social groups in the colony wide interaction network aggregated over 11 days. The optimal number of social groups, given by the maximum of the soft modularity, is two for all colonies. (**b**): Optimal number of groups as a function of the day for the colony wide interaction network aggregated over one day. On average over all colonies, this number is two in 91% of the days and three in the other 9% of the days.

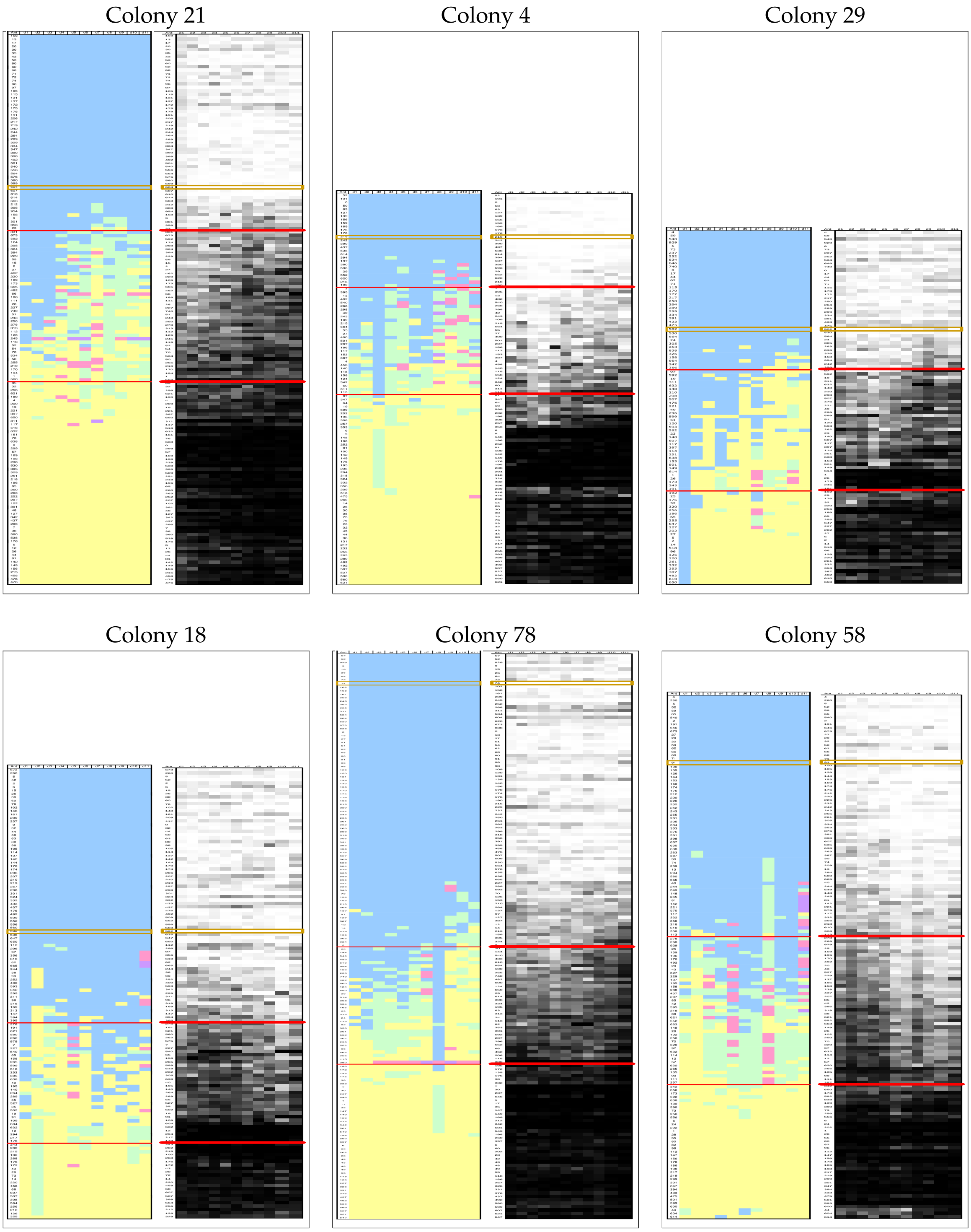

FIGURE 1.3: **Membership of ants in different groups using two different algorithms**. For each colony, the left column shows the three non-overlapping groups that Mersch et al. (2013b) identified with Infomap and the right column the two overlapping group we identified with FacetNet. For those two columns, the ant order is the same: based on the ant order of the Infomap column. For each column: x-axis: time [day], y-axis: ants. The red lines separate the groups from Mersch et al. (2013b): top group: nurses (queen's line with brown frame), middle group: cleaners, bottom group: foragers. For Infomap: Each color corresponds to a different group (no overlap allowed). For FacetNet: Level of black = social maturity.

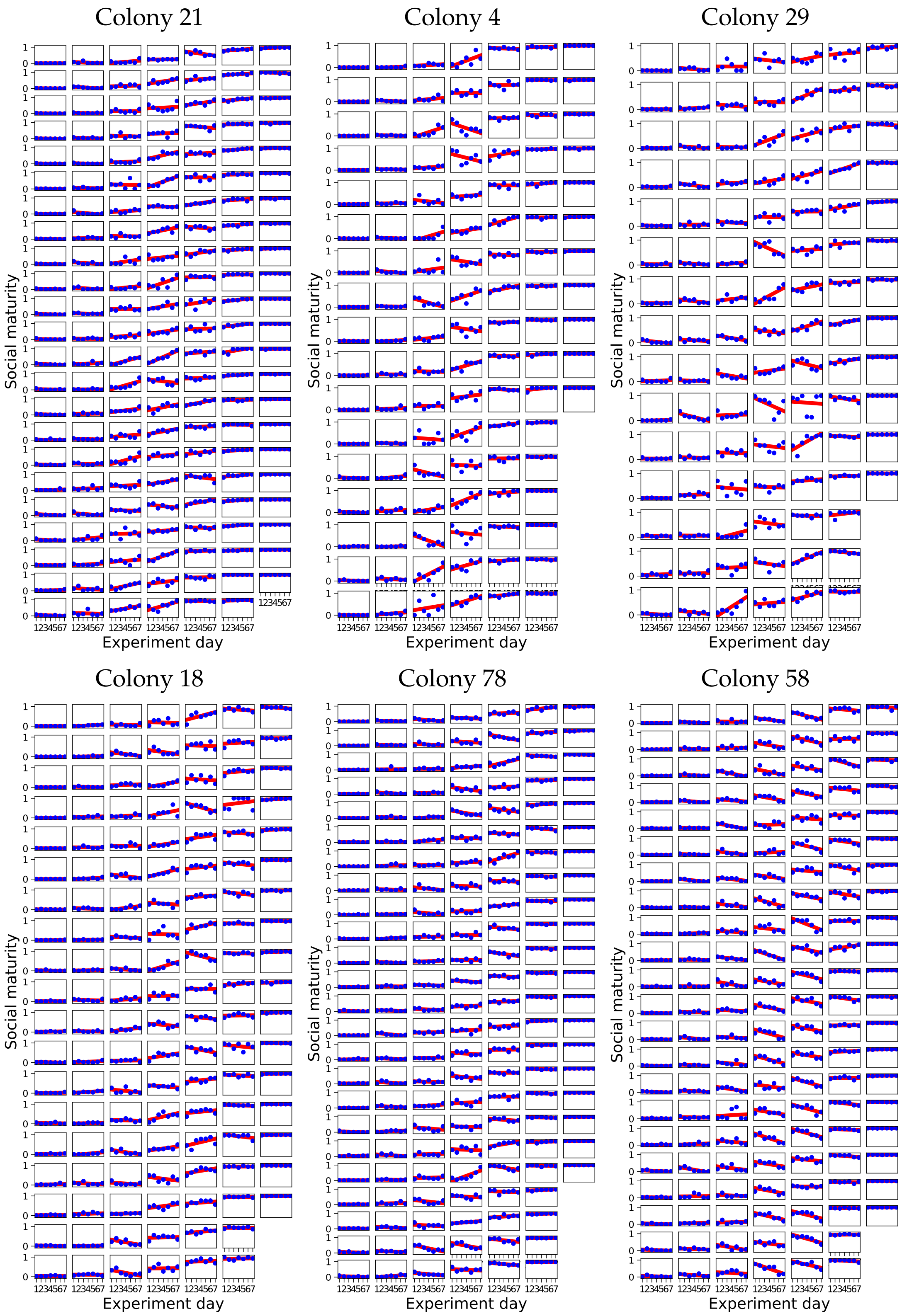

FIGURE 1.4: **Time series of social maturity values for all tracked workers in the six colonies.** Daily social maturity $S(i,t)$ over the seven-day training period. Each panel represents a different ant. Panels are sorted (from top to bottom and then from left to right) by increasing average social maturity over the entire seven-day period. The red line is a least-squares linear regression.

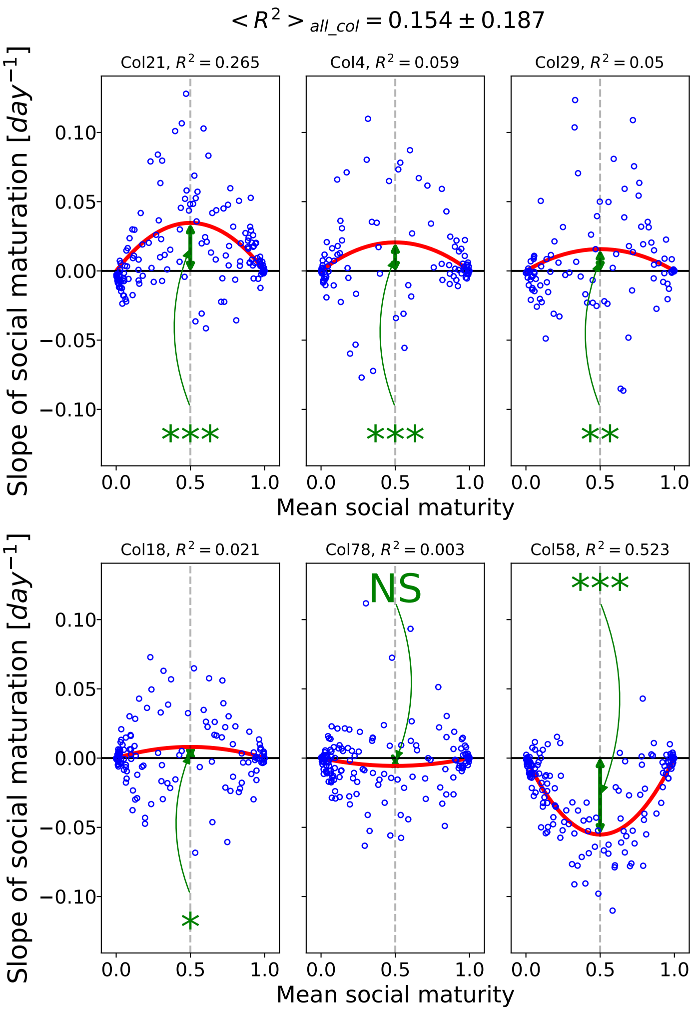

FIGURE 1.5: **Social dynamics of the workers in the six colonies during the seven-day training set.** Slope of linear regression of social maturity upon the seven days as a function of the seven-day mean social maturity. Each panel represents a different colony, each point a different ant. Red curve shows the "hill function" that fits this data and the green arrow shows the unique parameter (the expected maximum social maturation rate, m_{max}) of the hill function. In green: significance codes for p-value of m_{max}: $*** = [P < 0.001]$, $** = [P < 0.01]$, $* = [P < 0.05]$, $NS = [P > 0.05]$. R^2 is the coefficient of determination for each colony. $< R^2 >_{all\_col}$ is the mean ± standard deviation of the R^2 of all colonies.

TABLE 1.1: **Statistics on Fig. 1.5 and full social transition times (t_{FT}).** Expected maximum social maturation rate $m_{max} \pm SE$ (standard error), its t-statistic, degrees of freedom df ($N_{ants} - 1$), corresponding (two-sided) p-value (P) and $t_{FT} \pm SE$ the time an ant would take to do the full transition (nurse to forager social group or reverse):

	Colony 21	Colony 4	Colony 29	Colony 18	Colony 78	Colony 58
m_{max}[day^{-1}]	0.035 ± 0.003	0.021 ± 0.006	0.016 ± 0.005	0.008 ± 0.004	-0.006 ± 0.003	-0.055 ± 0.003
t-statistics	10.14	3.71	2.93	2.14	−1.76	−19.75
df	158	111	100	129	162	150
P	$7 \cdot 10^{-19}$	$3 \cdot 10^{-4}$	$4 \cdot 10^{-3}$	0.03	0.08	$1 \cdot 10^{-43}$
T_{FT} [day]	100 ± 10	168 ± 45	220 ± 75	427 ± 199	612 ± 347	63 ± 3

TABLE 1.2: **Results of the statistical comparison of the sigmoidal model with each alternative model**. For more details on each alternative model and statistical tests, see Materials and methods section 1.5.4.:

Competing model name ->	Colony mean	Ant mean	Colony slope	Ant slope
Probability (p-value) that, overall **on all ants of all colonies**, the competing model has a better predictive power than the sigmoidal model ->	$P < 10^{-111}$	$P < 10^{-4}$	$P < 10^{-19}$	$P < 10^{-13}$

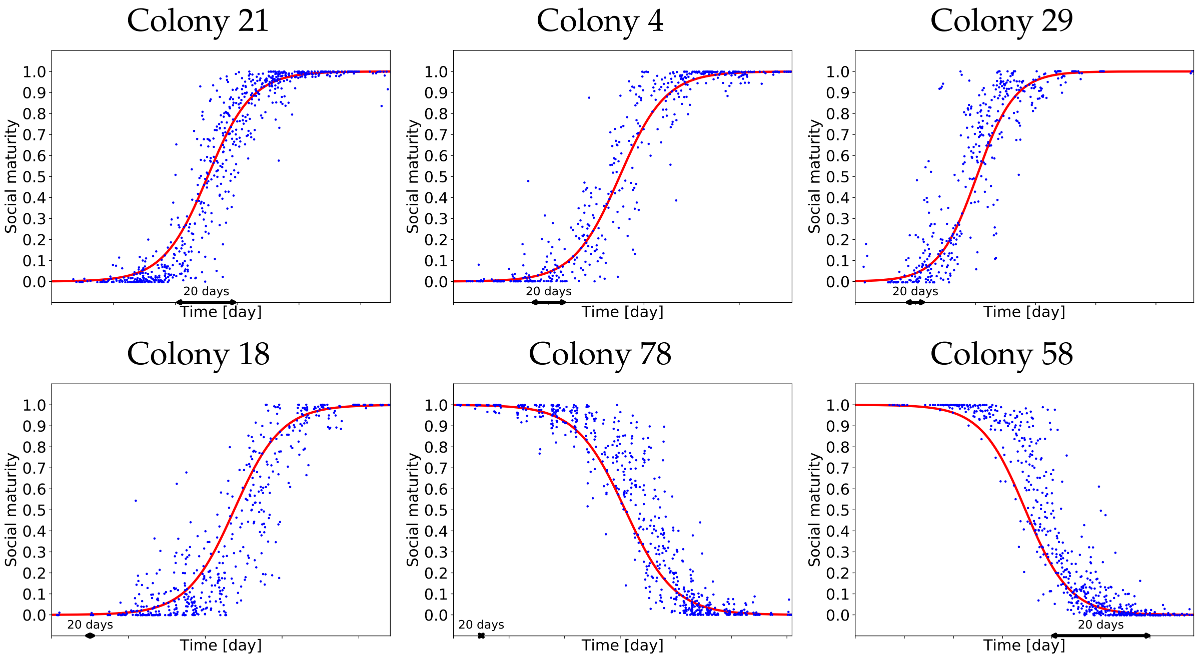

FIGURE 1.6: **Sigmoidal model predictions of the social maturity compared to observed future values.** Each panel represents a colony. For each panel, overall maturation curve constructed with the seven-day training period in red overlaid with the individual short-term social maturity during the four-day validation period (blue points).

1.3 Discussion

Our results show that unperturbed colonies of *C. fellah* comprise two overlapping social groups. In contrast, Mersch et al. (2013b) found three non-overlapping groups on the same dataset. This difference is explained by the fact that in our analysis we allowed for overlap in the social group analysis and that Mersch et al. (2013b) did not allow for overlap. In our analysis, the overlap is not imposed, it is simply allowed. Therefore, if non-overlapping groups would best describe the social structure, we would have detected it. For this reason, our analysis shows that an overlapping social group structure describes our daily ant social networks better than a non-overlapping social group structure. Therefore, individuals that are socially in between the nurse and the forager social groups should be viewed as forming a part of both groups at the same time rather than as a third separate group.

Because our model comparisons showed that the sigmoidal model is significantly more predictive than alternative models that assumed a linear change or no change at all, we showed that social maturation of a *C. fellah* worker follows a sigmoid (slow-fast-slow) during the lifetime of the worker. Therefore, the rate of social maturation varies over the lifetime of a worker. Maturation starts slowly, while the ant interacts with the nurse social group (social maturity close to zero). Then the social maturity accelerates to a maximum during social transition. At the middle of the social transition, the ant is interacting approximately as much with the nurse and the forager social group (social maturity ≈ 0.5). Finally, maturation slows as the ant interacts more and more with the workers of the forager social group (social maturity close to one). Thus, our analyses show that social maturation should be envisioned as a continuous movement on the social network on which ants gradually move from the nurse to the forager social group by gradually increasing their interaction frequencies with foragers compared to their interactions frequencies with nurses (i.e. gradual increase of social maturity). This sigmoidal dynamic could be caused by positive feedback being initially dominant, until the rate of maturation reaches a maximum (inflection point of the sigmoid) when negative feedback would start to dominate. Such two-stage slow-fast-slow non-linear sigmoidal dynamics are typical when regulatory mechanisms are present (Thomas et al., 1995), such as in population growth (Verhulst, 1845) and tumor growth (Laird, 1964), and suggest that, in our case of division of labor in social insects, social interactions play a regulatory role. For division of labor, such a sigmoidal maturation has been proposed in a simulation model (O'Donnell and Bulova, 2007a). This model combines the widely accepted response threshold model for division of labor (Bonabeau et al., 1996) with social interactions. The model of O'Donnell and Bulova (2007a) simulates ants recruiting other ants for a task using social interactions. This model assumes that each interaction of a recruiting ant with a recruited ant decreases the recruited ant's threshold for a given task, and therefore increases the recruited ant's probability of performing the task, thereby creating positive feedback. Under this assumption, which does not contradict experimental evidences (Greene and Gordon, 2003; Pless et al., 2015; Razin et al., 2013; Robinson et al., 2009b), the rate of recruitment of workers to tasks in this model had a sigmoidal growth form. In addition, negative feedback counterbalances the positive feedback (Bonabeau et al., 1997) thereby stabilizing the colony to homeostasis (Thomas et al., 1995). In the case of the transition from the nurse to the forager social group, the negative feedback loop could take the form of a decrease of the stimulus level for the foraging task caused by the performance of the foraging task by a worker (Beshers and Fewell, 2001). This negative feedback loop could be due, for example, to the limited number of available foragers, satiation, food source exhaustion or crowding at the food source (Bonabeau et al., 1997).

In terms of between colony variations, although four colonies followed the expected (Hölldobler and Wilson, 1990; Lenoir, 1979; Mersch et al., 2013b; Robinson, 1992; Seeley, 1982; Wilson, 1976) nurse to forager social transition, the social dynamics of one colony (colony 58) was inverted and followed a forager to nurse social transition. This is a surprising result and requires further investigation. In particular, we will need to investigate whether this inversion in the social transition correlates with an inversion of the temporal polyethism, i.e. whether workers are switching from foraging tasks specialists to nursing tasks specialists. In addition, we will need to investigate whether unique colony-level features of colony 58 could explain this singular behavior. Such analyses of task performance transitions and colony level features, such as the spatial structure of the nest, will be undertaken in the following chapter (Chapter 2).

Our estimates of the full social transition time range between 63 and 612 days. Those estimates correspond to realistic *C. fellah* workers lifespan as they can live up to 1–2 years (Danielle Mersch, personal communication) and the oldest worker in all colonies was measured by Mersch et al. (2013b) to be at least 436 days old at the end of the experiment. These results comfort the validity of our sigmoidal model in describing a long-term process, thereby further validating this model.

In terms of within colony variations, the sigmoidal model does not require ants to start their transition from the nurse to the forager social group at the same age. In contrast, classical temporal polytheism (Hölldobler and Wilson, 1990; Wilson, 1968) assumes that behavioral castes are separated according to their age and that age is the driver of task change. However, experimental data (Mersch et al., 2013b) showed that the age distribution of each group overlaps greatly with some foragers being younger than some nurses. Therefore, experimental data argue in favor of a loose connection between age and division of labor and further suggest that temporal polyethism is a noisy process, and our sigmoidal model accounts for that. Since the transition from the nurse to the forager social group can occur at any age, future work could ask the question what induces an ant to start this transition.

The approach to analyze and predict social group transition presented in this chapter depends on our ability to clearly define the social maturity for all workers of the colony. Because we found two overlapping groups in our experiment, the social maturity is one number per ant and per day describing the extent to which the ant belongs to one of the two groups compared to the extent to which the ant belongs to the other group. Following this logic, if in another system (for example another species of social insects) more than two groups are found, the social maturity would become a $(N-1)$-dimensional vector, where N is the number of groups. In our case of two groups, the curve that shows the transition from one group to another was a sigmoidal function in a two-dimensional space (one dimension for social maturity, one dimension for time). In the case of N groups the curve that would show the transitions between groups would be a function in a N-dimensional space ($N-1$ dimensions for social maturity, one dimension for time). The question whether this multidimensional curve would be a multidimensional sigmoidal remains open. Overall, our approach should therefore be generalizable to cases in which there are more than two groups.

Finally, our analyses reveal that there is no need to run long-term experiments to get information on long-term dynamics. With only seven days of tracking, we were able to deduce the current social maturity of a worker and determine its likely lifetime social maturation which we showed to be continuous, between two overlapping groups and sigmoidal. Moreover, we can deduce the time it would take an ant to do the full social transition and predict future social group membership (social maturity).

1.4 Individual contributions

RB did the analysis, under the supervision of DM, PD and LK. RB wrote the chapter, under the supervision of DM and LK. DM, AC and LK provided the dataset (Mersch et al., 2013b) used for this analysis.

1.5 Materials and methods

1.5.1 Description of the dataset

To study the dynamics of ants' social interactions, we used the first 11 days of the dataset of Mersch et al. (2013b) consisting of six *Camponotus fellah* unperturbed colonies (101 - 163 workers per colony) and which is available online as a Dryad data package (Mersch et al., 2013a). This dataset consisted of the position and orientation of all individuals twice per second (detection probability of $88 \pm 17\%$). Social interactions were then detected using a geometrical method that showed a close match between interactions detected by this method and visual analyses. As defined by this method, a social interaction between two individuals occurred if the angle between their bodies was greater than $70°$, and if they were more than 1 second in a position where at least one ant could reach the body of the other ant with its antennae. Such social interaction could for example represent trophallaxis (social sharing of food) or antennal contact.

The interaction networks used for our study consisted of the time series of the daily aggregated social interaction networks for each colony from Mersch et al. (2013b). In these networks, each node represents an ant, and the weight of the edges that link node pairs represents the total number of interactions between them on that day. The aggregation process, which consists of summing all interactions that happened between two ants during one day, leads to the loss of the temporal order of the interactions that occurred within a day (Blonder et al., 2012). This loss is of little concern here because we are interested in the long-term slow dynamics of division of labor (Mersch, 2016). In addition, our one-day aggregation window removes short-term and circadian fluctuations (Ingram et al., 2009; Lenoir, 1979; Mersch et al., 2013b).

1.5.2 Social group detection methods (OSLOM and FacetNet) and continuous group membership (social maturity)

To detect the social groups in the interaction network we ran the OSLOM (“Order Statistics Local Optimization Method”; Lancichinetti et al., 2011) and the FacetNet (“Framework for Analyzing Communities and EvoluTions in dynamic NETworks”; Lin et al., 2009) social group detection algorithms. Both algorithms could account for overlapping social group structure. OSLOM did not need the number of groups as an input, and FacetNet could output the group membership for each individual as a continuous number in the range $0 - 1$. This group membership describes the extent to which each individual belongs to each of the two overlapping social groups. A group membership of 0 indicates an ant that is *deeply embedded* in one of the groups (i.e., it interacts the most with other ants of this group compared to its interactions with the other group). A group membership of 1 indicates an ant that is deeply embedded in the other group. Any other value of this group membership indicates intermediary level of group membership. For example, a group membership of 0.5 indicates an ant that is *between the two groups*, i.e. that interacts as much with ants of both groups.

As it was shown that workers move from one group to the other as they age (Mersch et al., 2013b; Robinson, 1992; Seeley, 1982), we named the continuous group membership variable the *Social Maturity*. Because the social maturity is defined for each ant i, on each day t, we refer to it as $S(i, t)$. Considering that ants tend to specialize in nursing and associate more with nurses when they are young, and switch to foraging and associate more with foragers when older, $S(i, t)$ captures these interaction biases. Hence, $S(i, t) = 0$ indicates an ant that interacts the most with other nurses (average social maturity of the nurse group of Mersch et al. (2013b) 0.09) and $S(i, t) = 1$ indicates an ant that interacts the most with other foragers (average social maturity of the forager group of Mersch et al. (2013b) 0.91).

1.5.3 Computation of t_{FT}, the full social transition time

The *full social transition time* (t_{FT}) is defined as the time it would take an ant to do the full social transition from the lowest to the highest social maturity (if $m_{max} > 0$) or from the highest to the lowest social maturity (if $m_{max} < 0$). Theoretically, the lowest possible social maturity is $S(i,t) = 0$ and the highest possible social maturity is $S(i,t) = 1$. However, because of the asymptotic properties of the sigmoid, using such values would imply that $t_{FT} = \infty$ for any values of m_{max} and therefore any comparison of t_{FT} between colonies would be impossible. To address this limitation, the social maturity was (slightly) rescaled in each colony such that the lowest possible social maturity became $S(i,t) = \epsilon$ and the highest possible social maturity became $S(i,t) = 1 - \epsilon$, with $\epsilon > 0$ but very small ($\epsilon \ll 1$). For the comparison of t_{FT} between colonies, ϵ had to be set to the same value for all colonies that we chose at $\epsilon = 0.001$.

1.5.4 Predictions and statistical comparison to four alternative models

We used the sigmoidal model fitted on the training dataset to predict future social maturity values for each ant (Fig. 1.7). To assess the predictive power of the sigmoidal model, it was important to separate the data used for training (days 1–7) to the data used for validation (days 8–11) and that the validation dataset was solely used to compare the prediction of the model to alternative models. This practice is in accordance with the practice for fitting predictive models of other complex systems (Etter et al., 2013). We chose to separate the 11-day data into seven days for training and four days for validation, because a visual inspection of the plots showing the social dynamics

(Slope of linear regression of social maturity upon time as a function of the mean social maturity) for an increasing time window suggested that seven days was the minimum time range to assess the social dynamics and therefore train the sigmoidal model.

To predict the future social maturity of a given ant, we first had to know its *initial location*, here defined as its x (time) and y (social maturity) coordinates at the middle of training set (day 4), within the overall sigmoidal maturation curve. We inferred the initial location of each ant within the overall sigmoidal maturation curve (obtained from the seven-day training period) by intersecting the horizontal line defined by its seven-day average social maturity $S(i,t)$ and the fitted sigmoidal curve (Fig. 1.7d). We then used the sigmoidal curve to predict future social maturity values for a given ant by using the initial location of the ant on this curve and inferring the predicted change from the curve (Fig. 1.7e).

To test the predictive power of the sigmoidal model, we compared it to the predictive power of four alternative models that either assumed a linear change or no change at all. The assumptions and description of each of those models are summarized on Table 1.3 and are described in detail in the following paragraphs.

The first alternative model, referred to as *colony mean*, assumes that all ants of a given colony had the same social maturity (uniform $S(i,t)$) at all time (constant $S(i,t)$). This situation would arise if all ants interacted uniformly with each other at all times. Here, the forecast for each ant is equal every day to the mean of the social maturity of all ants of the colony during the training set.

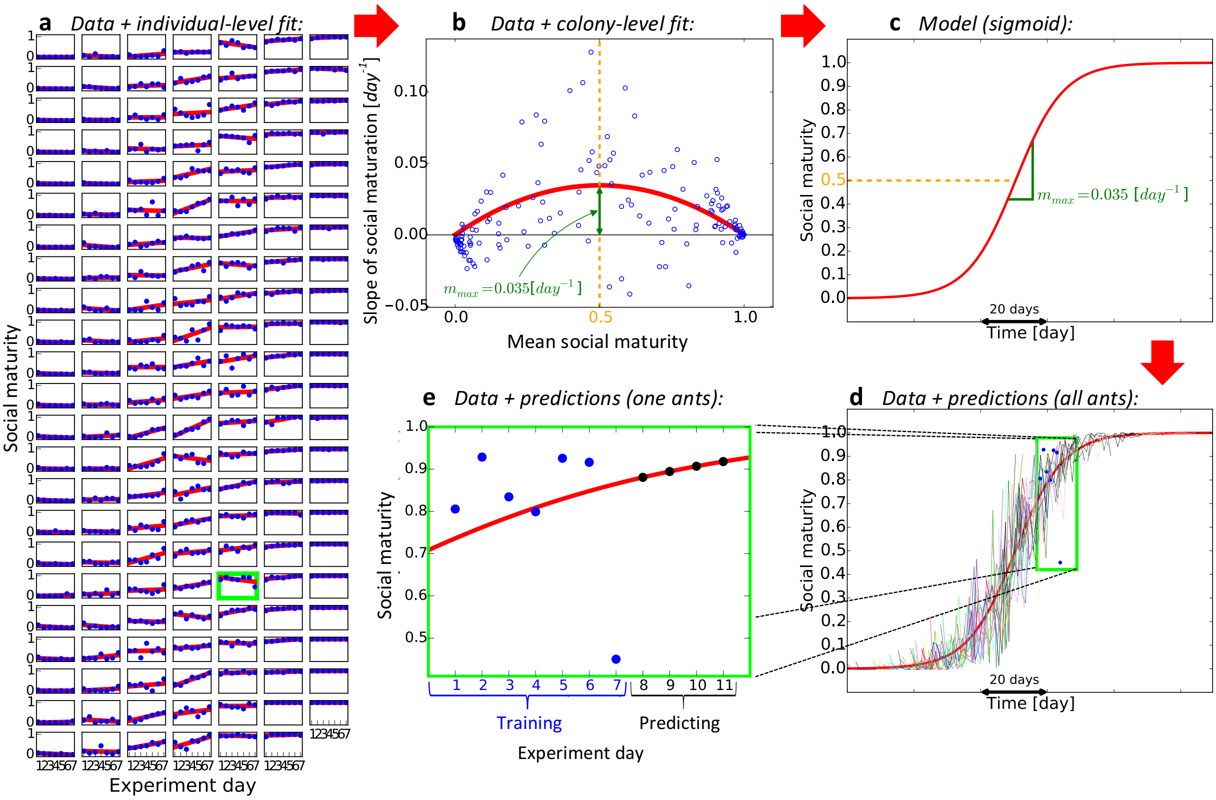

FIGURE 1.7: **Sigmoidal social dynamics: modeling and prediction steps of individual social maturation for one colony of 160 ants.** (**a**): Daily social maturity $S(i,t)$ over the seven-day training period. Each panel represents a different ant. Panels are sorted (from top to bottom and then from left to right) by increasing average social maturity over the entire seven-day period. The red line is a least-squares linear regression. The ant in the green rectangle is the ant highlighted in panels d and e. (**b**): Rate of social maturation as a function of the average social maturity. Points show the slope of the linear regression $m(i)$ (y-axis) and the seven-day average $S(i,t)$ (x-axis) for each ant i. The red line shows the "hill function" that fits this data, with a single parameter m_{max} corresponding to the expected maximum social maturation rate. (**c**): Sigmoid function, which represents the long-term social maturation dynamics of a typical ant. (**d**): Overlay of individual short-term social maturation dynamics during the seven-day training period (colored lines) with the overall maturation curve (red line). (**e**): Enlargement of the trajectory and sigmoid overlay for a single ant (ant 32). Blue dots represent the seven values of social maturity during the seven days of video tracking and the black dots the four predicted values for the next four days.

The second alternative model, referred to as *ant mean*, assumes again that social maturity does not vary over time (constant $S(i,t)$), but allows social maturity to vary between individuals. This situation would arise if all ants interacted with the same individuals at all times. Here, the forecast for each ant is equal every day to the mean of the social maturity of the ant during the training set.

TABLE 1.3: **Summary table of the four alternative models to explain the social dynamics**:

Competing model name ->	Colony mean	Ant mean	Colony slope	Ant slope
Competing model assumptions (for each colony) ->	Uniform and constant social maturity for all ants	Constant social maturity for each ant	Uniform and constant social maturation rate for all ants	Constant social maturation rate for each ant
Competing model description (for each colony) ->	Mean of all ants	Mean of each ant	Line with same slope (mean of the slope of all ants) for all ants	Slope given by linear regression for each ant

The third model, referred to as *colony slope*, allows again social maturity to vary between individuals, but also assumes that social maturity changes linearly over time (constant rate of $S(i,t)$) with the same slope for all ants (uniform rate of $S(i,t)$). This model represents the situation where all ants change their interaction partners from one group to another at the same constant rate. For each ant, the forecast is given by a line that passes, at the middle of the testing set (day 4), through the ant's mean social maturity calculated from the training dataset. For each ant, this line has a slope equal to the mean of the slopes of all ants. Like the sigmoidal model, this model has N_{ants} individual-level parameters (mean social maturity for each ant) and one colony-level parameter (mean slope of all ants). Hence, it can be seen as a linear equivalent of the sigmoidal model.

Finally, the fourth alternative model, referred to as *ant slope*, allows again social maturity to vary between individuals and assumes again that social maturity changes linearly over time (constant rate of $S(i,t)$). However, unlike the colony slope model, the rate of change of social maturity (slope of the linear regression) is allowed to vary between ants. This model represents the situation where all ants change their interaction partners from one group to another at a rate that is constant in time for a given ant but allowed to vary between ants. For each ant, the forecast is given by a line that passes, at the middle of the testing set (day 4), through the ant's mean social maturity calculated from the training dataset. For each ant, this line has a slope given by the linear regression of the social maturity of the ant during the training set.

To quantify the predictive power of each model, we compared its forecast for the last four days of the data (validation dataset, black dots in Fig. 1.7e) with the observed values for those four days. We then estimated the *prediction error*, which is inversely related to the prediction power, as the sum of the absolute differences between the predictions and the observed values. To test whether the sigmoidal model had a lower prediction error than an alternative model, we performed a two-sided Wilcoxon paired test comparing, for all ants of one colony, the prediction error of the sigmoidal model with the prediction error of the alternative model. For each alternative model, we then obtained one p-value per colony. We then used Fischer's method (Fisher, 1954; Hedges and Olkin, 1985; Sokal and Rohlf, 1995) to combine all the p-values of all colonies into one p-value per alternative model.

1.6 Appendix

1.6.1 Separation of each colony in maturing and dematuring ants

The sigmoidal model is a useful simplification of the social maturation because it leads to successful predictions of ants future social maturity. However, in the four colonies where a significantly positive sigmoidal social maturation (i.e. significantly positive m_{max}) had been detected, there were still ants with a negative slope of social maturation, i.e. ants *dematuring* from the forager to the nurse social group (Fig. 1.5). Reciprocally, in the colony where a significantly negative sigmoidal social maturation (i.e. significantly negative m_{max}) has been detected, there were still ants with a positive slope of social maturation, i.e. ants *maturing* from the forager to the nurse social group (Fig. 1.5).

To test whether it is the proportion of ants maturing (or dematuring) that can explain the inter-colony variance in m_{max}, we tested whether there is a significant correlation between m_{max} and the proportion of ants maturing (compared to the total number of ants in the colony, that are either maturing or dematuring [no ants have a slope zero]). We found that this correlation was indeed significant, positive and close to a total positive linear correlation of Pearson's $r = 1$ (Pearson's $r = 0.98$, $P = 0.001$; Fig. 1.8a). Consistently, the percentage of the variance in m_{max} that is predictable from the proportion of ants maturing was 97% (i.e. the coefficient of determination $R^2 = 0.97$). In each colony, to measure separately the social maturation rate of the ants maturing and the social maturation rate of the ants dematuring, we fit one "hill function" for the ants with a positive slope of social maturation and another one for the ants with a positive slope of social maturation (Fig. 1.9). We found that the correlation between m_{max} of the single hill function (fitted for all ants of the colony; see Fig. 1.5) and m^{+}_{max} (i.e. m_{max} fitted for the ants with a positive social maturation slope) was significant (Pearson's $r = 0.89$, $P = 0.017$; $R^2 = 0.8$; Fig. 1.8b). Similarly, the correlation between m_{max} of the single hill function and m^{-}_{max} (i.e. m_{max} fitted for the ants with a negative social maturation slope) was also significant (Pearson's $r = 0.9$, $P = 0.014$; $R^2 = 0.81$; Fig. 1.8c). Overall, more (i.e. 97%) inter-colony variance in m_{max} (single hill function) was predictable from the proportion of ants maturing than from m^{+}_{max} (80% of variance) or from m^{-}_{max} (81% of variance). However, all three values (proportion of ants maturing, m^{+}_{max} and m^{-}_{max}) could significantly explain the inter-colony variance in m_{max}.

This analysis therefore gives us a more complete interpretation of the m_{max} (single hill function) used throughout this chapter: A colony with a higher m_{max} will contain a higher proportion of ants maturing, its maturing ants will mature faster and its dematuring ants will demature slower than a colony with a lower m_{max}.

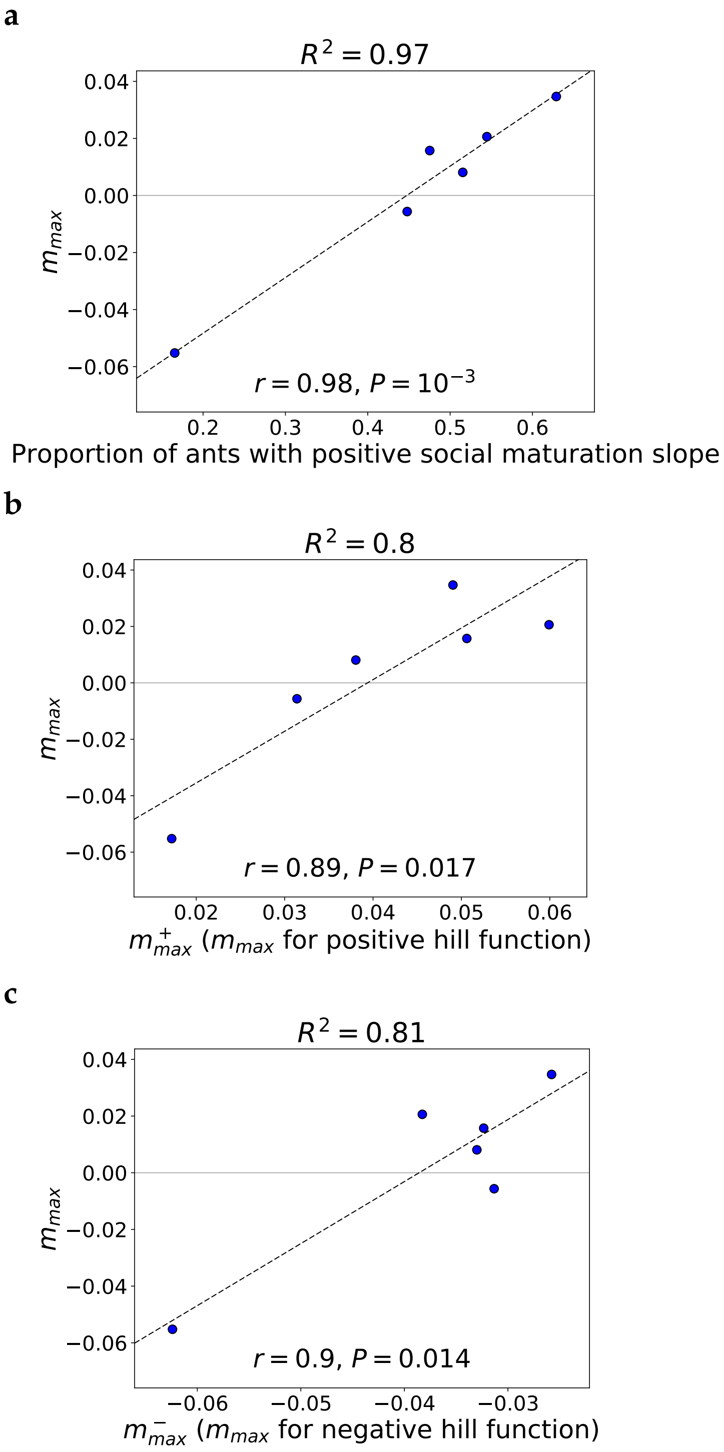

FIGURE 1.8: **Correlation between m_{max} of the single hill function (fitted for all ants of the colony; see Fig. 1.5) and the parameters of the double hill function (fitted separately for the ants with a positive and a negative social maturation slope; see Fig. 1.9).** (**a**, **b** and **c**): Each point represents a different colony. r is the Pearson correlation coefficient and is followed by its p-value (P). R^2 shows the proportion of the variance in the y-axis that is predictable from the x-axis. y-axis: m_{max} fitted for all ants of the colony. (**a**): x-axis: proportion of ants with positive social maturation slope. (**b**): x-axis: m_{max} fitted for the ants with a positive slope (m^+_{max}; see Fig. 1.9). (**c**): x-axis: m_{max} fitted for the ants with a negative slope (m^-_{max}; see Fig. 1.9).

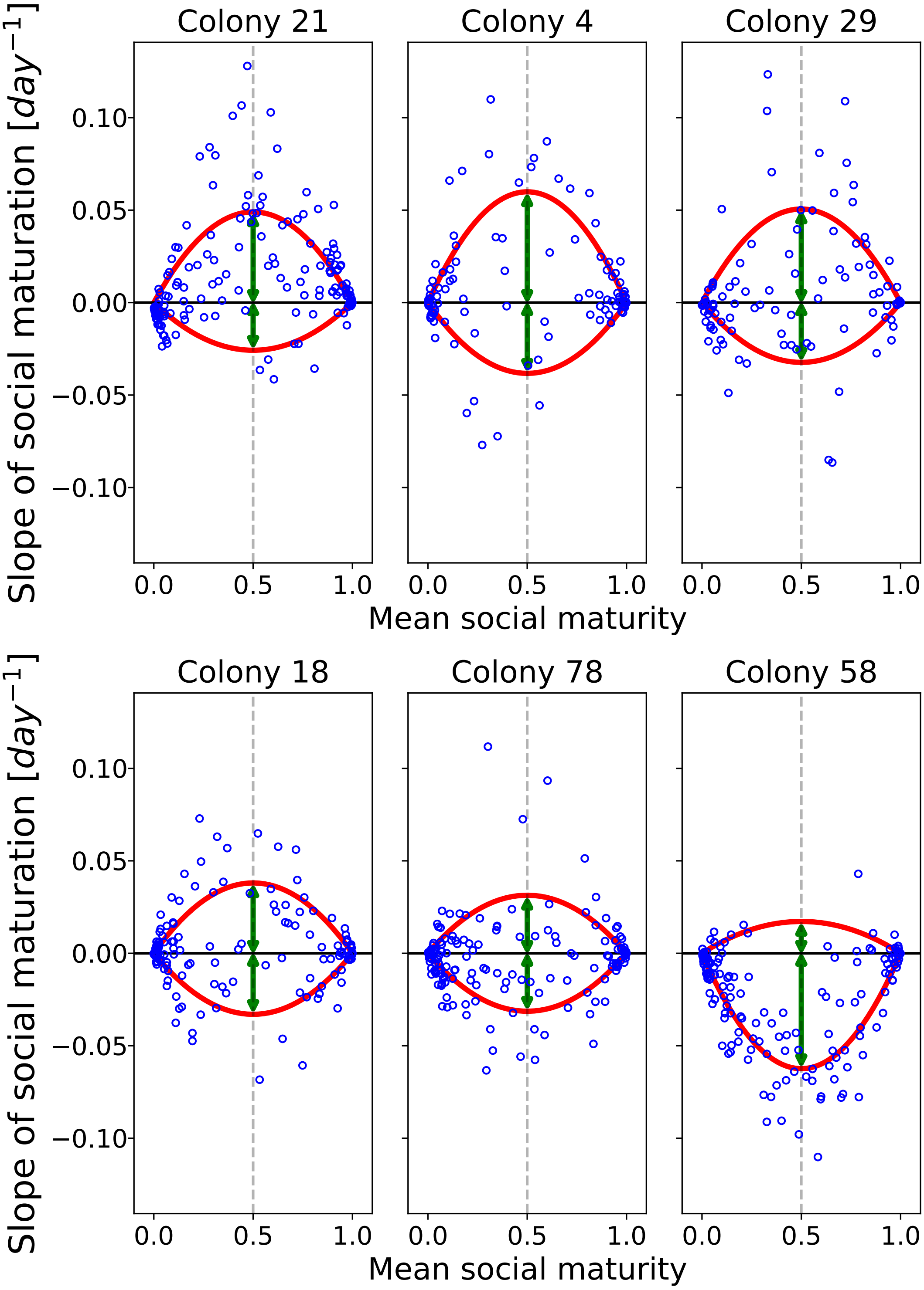

FIGURE 1.9: **Social dynamics with separated fit for maturing and dematuring workers**. Slope of linear regression of social maturity upon the seven days as a function of the seven-day mean social maturity. Each panel represents a different colony, each point a different ant. For each panel, we fit one "hill function" (red curve) for the points with a positive slope (*maturing* ants) and another one for the points with a negative slope (*dematuring* ants). For each colony, each of the two hill functions has a single parameter (shown with green arrows) corresponding to the expected maximum social maturation rate of either the maturing (m^{+}_{max}) or the dematuring (m^{-}_{max}) ants of the colony.

Chapter 2

Dynamics of division of labor and social interactions in ants and their relation to spatial segregation

Collaborators on this chapter:

Raphaël Braunschweig; Danielle Mersch; Mohamed Kafsi; Matthias Grossglauser; Patrick Thiran; Alessandro Crespi; Laurent Keller

2.1 Introduction

The analyses of Chapter 1 considered the dynamics of individual ants as they changed position in the social interaction network and moved from the *nurse social group* (the social group containing the queen and the nurses) to the *forager social group* (the social group containing the foragers). We called this dynamics the *social dynamics*. To quantify the social dynamics, we devised the *social maturity* index, which was defined to have a value of 0 for the individuals the most deeply embedded in the nurse social group (i.e. highest number of interactions with other ants in the nurse social group relative to their number of interactions with the ants of the forager social group) and a value of 1 for the individuals the most deeply embedded in the foragers social group. However, the primary cause of the ecological success of social insects is division of labor (Hölldobler and Wilson, 1990), which is influenced by the social interactions (Greene and Gordon, 2003; Pless et al., 2015; Razin et al., 2013; Robinson et al., 2009b, Mersch et al., 2013b, Fewell, 2003; Mersch, 2016; O'Donnell and Bulova, 2007b; Robinson, 1992). Nevertheless, how social interactions contribute to division of labor in ants is still poorly understood (Fewell, 2003; Mersch, 2016; O'Donnell and Bulova, 2007b; Robinson, 1992). So far, mainly theoretical and simulation models have proposed mechanisms that could link social interactions to workers' task (Beshers and Fewell, 2001; Bonabeau et al., 1998; Huang and Robinson, 1992; Kang and Theraulaz, 2016; Naug and Gadagkar, 1999; O'Donnell and Bulova, 2007a; Pacala et al., 1996; Razin et al., 2013, Bonabeau et al., 1996). In those models, information about task needs is transferred through social interactions which can affect task switching decisions. Several studies found experimental evidence of the mechanisms that could link workers' task to their social interactions (Greene and Gordon, 2003; Pless et al., 2015; Razin et al., 2013; Robinson et al., 2009b, Mersch et al., 2013b). Interactions with returning foragers for individuals close to the nest entrance have been shown to correlate with the probability of leaving the nest (Pless et al., 2015). Moreover, Greene and Gordon (2003) found that, in *Pogonomyrmex barbatus*, dropping glass beads coated with cuticular hydrocarbons of patrollers into the nest stimulated a higher number of foragers to leave the nest than beads with nest-maintenance-worker hydrocarbons or beads without any hydrocarbons. In addition, this number of foragers stimulated to leave the nest by the patrollers hydrocarbons coated beads was similar to the number of foragers stimulated to leave by live patrollers returning to the nest. Thus, when a worker interacts with a nestmate, it recognizes its task group identity from its task-group-specific cuticular hydrocarbons, which informs its decision whether to perform a given task or not. Another experimental evidence of mechanisms linking the workers task performance to their social interactions is a study of Razin et al. (2013). The authors showed that reliable recruitment for foraging could be achieved in *Cataglyphis niger* through a simple interaction between the recruiter, which maintains its speed before and after the interaction, and the recruitee, which increases its speed in response to the interaction. However, to get a complete picture of the link between division of labor and social interactions in ants, one would need to track all social interactions and task performances of an entire ant colony. Such tracking was first achieved in Mersch et al. (2013b) who showed, by tracking the position and orientation every 0.5 seconds of all ants of six colonies of *Camponotus fellah* over 41 days, that there is a match between tasks, social groups and spatial location. However, in order to understand how the division of labor could be regulated, the relationship between the *dynamics* (i.e. the change over time) of task and social interaction would need to be analyzed.

Therefore, the first aim of this chapter is to investigate the relationship between the social dynamics and the *task dynamics*, which is the change over time of the tasks of the ants. Similarly to what we did in Chapter 1 for the social dynamics, to quantify the task dynamics, we devised the *task specialization* index, which is defined as the index of specialization of each worker in two key tasks, foraging and brood nursing. For each worker, this index uses the number of visits of the worker to the foraging arena and the number of visits of the worker to the brood pile. To identify workers that change task from one day to the next and quantify the task dynamics of each worker of the colony, we measured the task specialization of each worker every day.

The social maturity and task specialization indexes are both individual-level (local) properties. Through self-organization those individual-level properties and their dynamics give rise to colony-level (global) structures (Bonabeau et al., 1997). In our case, the distance between the nest entrance and the brood pile, referred to as *entrance-brood* *distance*, constitutes an important colony-level measure, because we are interested in the nurse to forager transition and this distance quantifies the spatial separation between the zone of the nest (the brood pile) where the nurses perform their task (brood care) and the zone of the nest (the nest entrance) where the foragers perform their task (leave the nest to forage or come back from a foraging trip). Individual ants show *spatial fidelity* — the tendency to stay in and come back to the same region of the nest (Heyman et al., 2017; Sendova-Franks and Franks, 1993; Sendova-Franks and Franks, 1995). In addition, ants show *spatial segregation* which is a colony level property where the spatial distributions of ants of the same task are similar to one another (Mersch et al., 2013b). To assist and maintain this spatial segregation and spatial fidelity, the ants use specific chemicals for each task group (Heyman et al., 2017). The ants deposit, actively or passively, those chemicals on the floor and can then recognize those chemicals, therefore guiding the ants' movement within the dark nest. However, how those colony-level properties (entrance-brood distance and spatial segregation) are related to the social and the task dynamics is still an open question. Attempting to answer this question might give us more insight on how self-organization works in social insects and constitutes the second aim of this chapter. To quantify the spatial segregation of the ants, we define the *spatial segregation zones* (SSZs) as the spatial distributions in which ant workers spatially segregate. We used a slightly modified version of the machine-learning algorithm devised in Kafsi et al. (2016) to automatically identify and count the different SSZs, and assign each worker to its most likely SSZ, objectively and without prior purely based on the spatial distributions of all ants.

2.2 Results

To quantify the task specialization change over time for each ant, we performed a least-squares linear regression of the task specialization $T(i,t)$ (defined in Materials and methods section 2.5.1) upon the 11 days of tracking, similarly to what we did for the social maturation in Chapter 1. To visualize the dynamics of task specialization of all ants of a colony, we represented each ant as a point in a scatter plot of the slope of the linear regression (which is an estimation of the task specialization rate) as a function of the 11-day average task specialization (Fig. 2.1a). Because we observe a positive "hill function" (slow-fast-slow) trend, which consists of slope zero (slow) at $T(i,t) = 0$ or 1 and maximum value (fast) reached at $T(i,t) = 0.5$, we then fitted a "hill function" on the data of this plot (For more details see Materials and methods section 2.5.2).

Using this 'hill function' fit (see Materials and methods section 2.5.2) we found that, for all colonies, individuals increased (on average) over time their task specialization index, meaning that they increased their number of visits to the foraging arena compared to their number of visits to the brood pile (Fig. 2.1a). This positive trend was significant (i.e. $m_{max}(Task)$ of the hill function significantly positive, $P < 10^{-7}$) for all colonies except colony 18 ($P = 0.056$). However, although four colonies contained mostly individuals that transited from the nurse to the forager social group (i.e. $m_{max}(Social)$ significantly positive, $P < 10^{-10}$), the social dynamics of two colonies (colonies 58 and 18) was inverted with most individuals transitioning from the forager to the nurse social group (i.e. $m_{max}(Social)$ significantly negative, $P < 10^{-6}$; Fig. 2.1b).

The social maturity ($S(i,t)$) and task specialization ($T(i,t)$) of the individual ants were positively correlated for each colony (mean of Spearman rank correlation coefficient across colonies $= 0.78$, standard deviation of Spearman rank correlation coefficient across colonies $= 0.07$, $P < 10^{-10}$; Fig. 2.2). The graphs of Fig. 2.2 also show that the variance in the social maturity decreased as task specialization increased, i.e. the data showed *heteroscedasticity*. This was an artifact of our measure of task specialization $T(i,t)$ because it was more coarse-grained than our measure of social maturity, especially for ants that did not leave the nest (see Materials and methods section 2.5.1 for more details). Despite this heteroscedasticity in the data, our correlation (between $S(i,t)$ and $T(i,t)$) results were still valid because we used the Spearman rank correlation test which is a rank-based non-parametric correlation test.

Similarly to Kafsi et al. (2016) (but without activity; see Materials and methods section 2.5.4), the number of SSZs found, using the maximization of the likelihood of the data, was $K = 3$. Comparing those three SSZs to the brood pile, nest entrance and foraging arena (Fig. 2.3) revealed that, for all six colonies, the three SSZs were roughly corresponding to: the brood pile and its surroundings (*nursing SSZ*), the foraging arena, the nest entrance and its surroundings (*foraging SSZ*), the intermediary region between the brood pile and the nest entrance (*intermediate SSZ*).

The overlap values between the different SSZs, represented by the edges of the networks of Fig. 2.4 and defined in Materials and methods section 2.5.5, showed that the overlap between the foraging and the nursing SSZs was lower than the overlaps of both SSZs with the intermediate SSZ (i.e. $O_{NF} < O_{NI}$ and $O_{NF} < O_{IF}$) for five out of the six colonies (i.e. all colonies except colony 58).

Comparing the individual-level task dynamics to the colony level spatial segregation showed that the expected maximum task specialization rate ($m_{max}(Task)$) was negatively correlated with the overlapping proportion of the SSZs (abbreviated O_{all} and defined in Materials and methods section 2.5.6; Pearson's $r = -0.93$, $P = 0.007$; Fig. 2.5a). In addition, $m_{max}(Task)$ was negatively correlated with the relative difference between O_{NI} and O_{IF} (Pearson's $r = -0.86$, $P = 0.028$; Fig. 2.5b). The smaller this relative difference the more balanced is the overlap of the intermediate SSZ with the nursing SSZ and the foraging SSZ. More details and the mathematical definition of this relative difference can be found in Materials and methods section 2.5.7 .

Furthermore, comparing the individual-level social dynamics to the colony level entrance-brood distance (Fig. 2.6) showed that the expected maximum social maturation rate, $m_{max}(Social)$, was positively correlated with the entrance-brood distance (Pearson's $r = 0.84$, $P = 0.036$; Fig. 2.7a). Similarly, the value of the overlap between the foraging and the nursing SSZs (represented by the edge between the nodes F and N of Fig. 2.4 and defined in Materials and methods section 2.5.5) was negatively correlated with the expected maximum social maturation rate (Pearson's $r = -0.82$, $P = 0.047$; Fig. 2.7b).

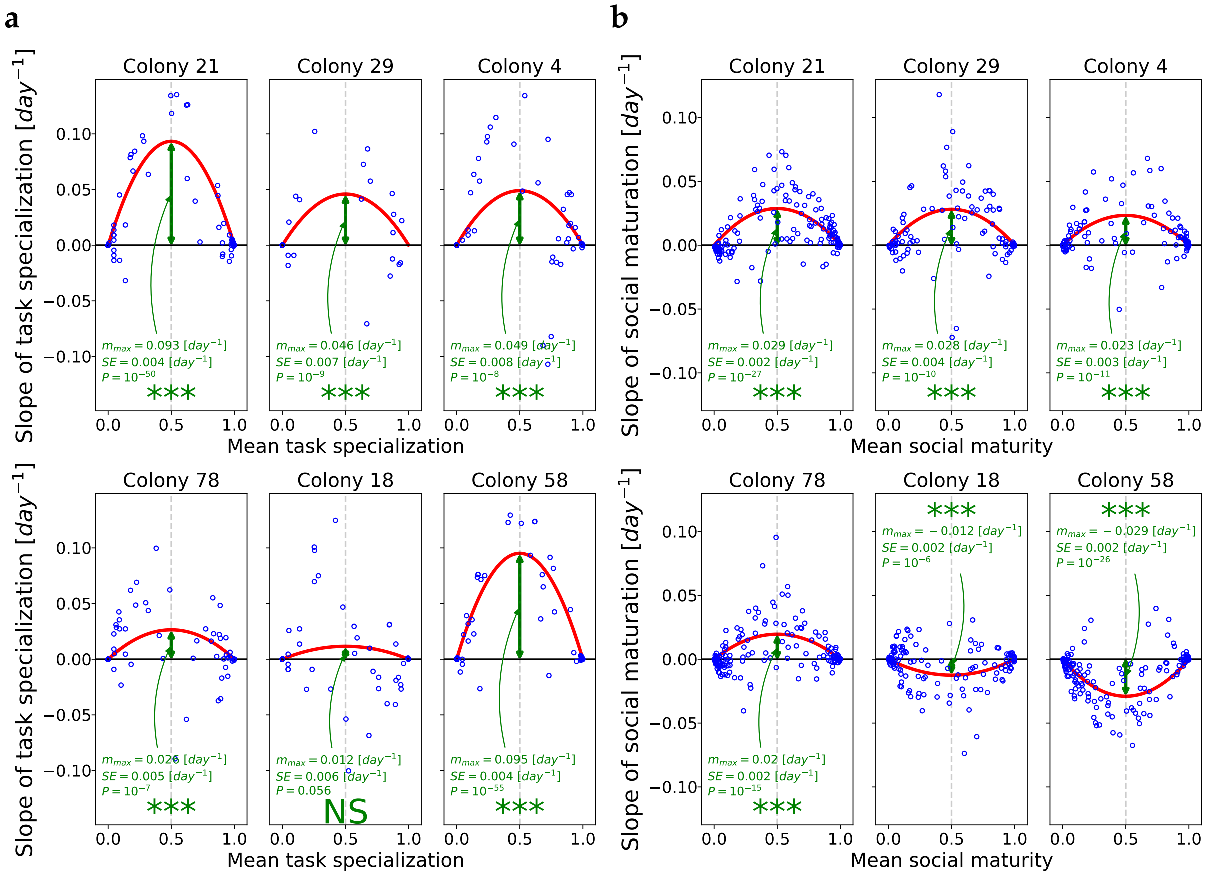

FIGURE 2.1: **Task and social dynamics.** (**a** and **b**): Each panel represents a different colony, each point a different ant. The red line shows the "hill function" that fits this data, with a single parameter m_{max} (in green), the expected maximum social maturation rate. SE and P (in green) indicate respectively the standard error and the p-value on m_{max}. Significance codes (in green) for the p-value for m_{max} : $*** = [P < 0.001]$, $** = [P < 0.01]$, $* = [P < 0.05]$, $NS = [P > 0.05]$. (**a**): Task dynamics for 11 days. (**b**): Social dynamics for 11 days.

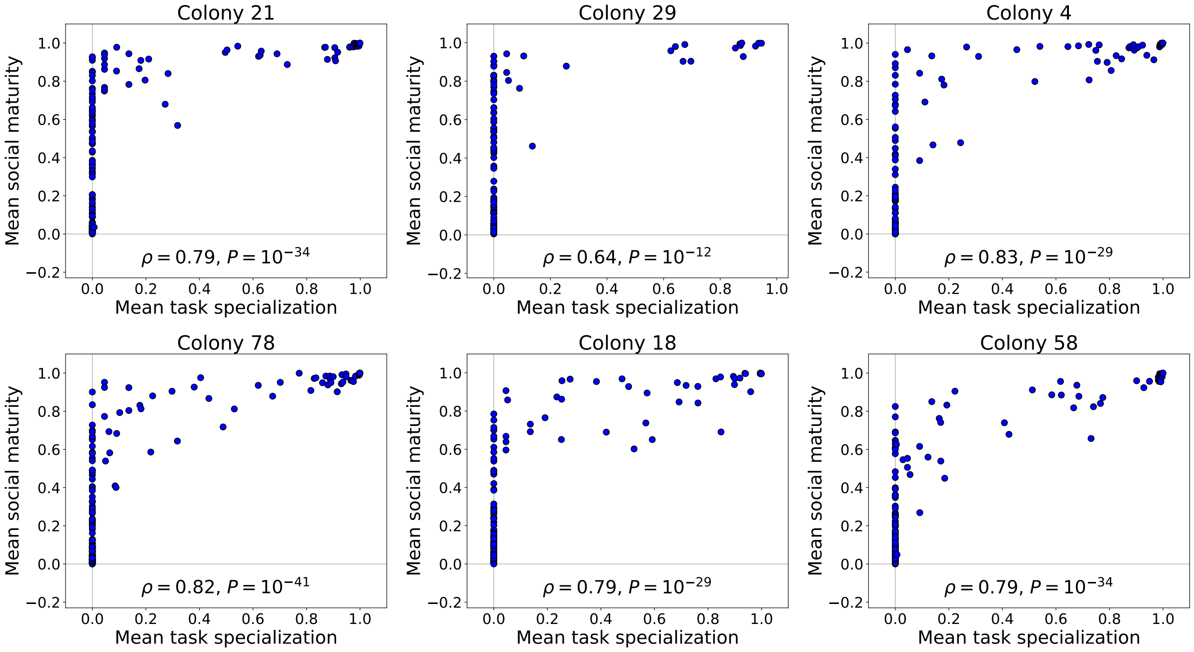

FIGURE 2.2: **Correlation between the mean social maturity and the mean task specialization value of the individual ants of each colony.** The mean is taken across all 11 days of the experiment. Each panel shows the values for a different colony. For each panel, each point represents a different ant and ρ is the Spearman rank correlation coefficient and is followed by its p-value (P).

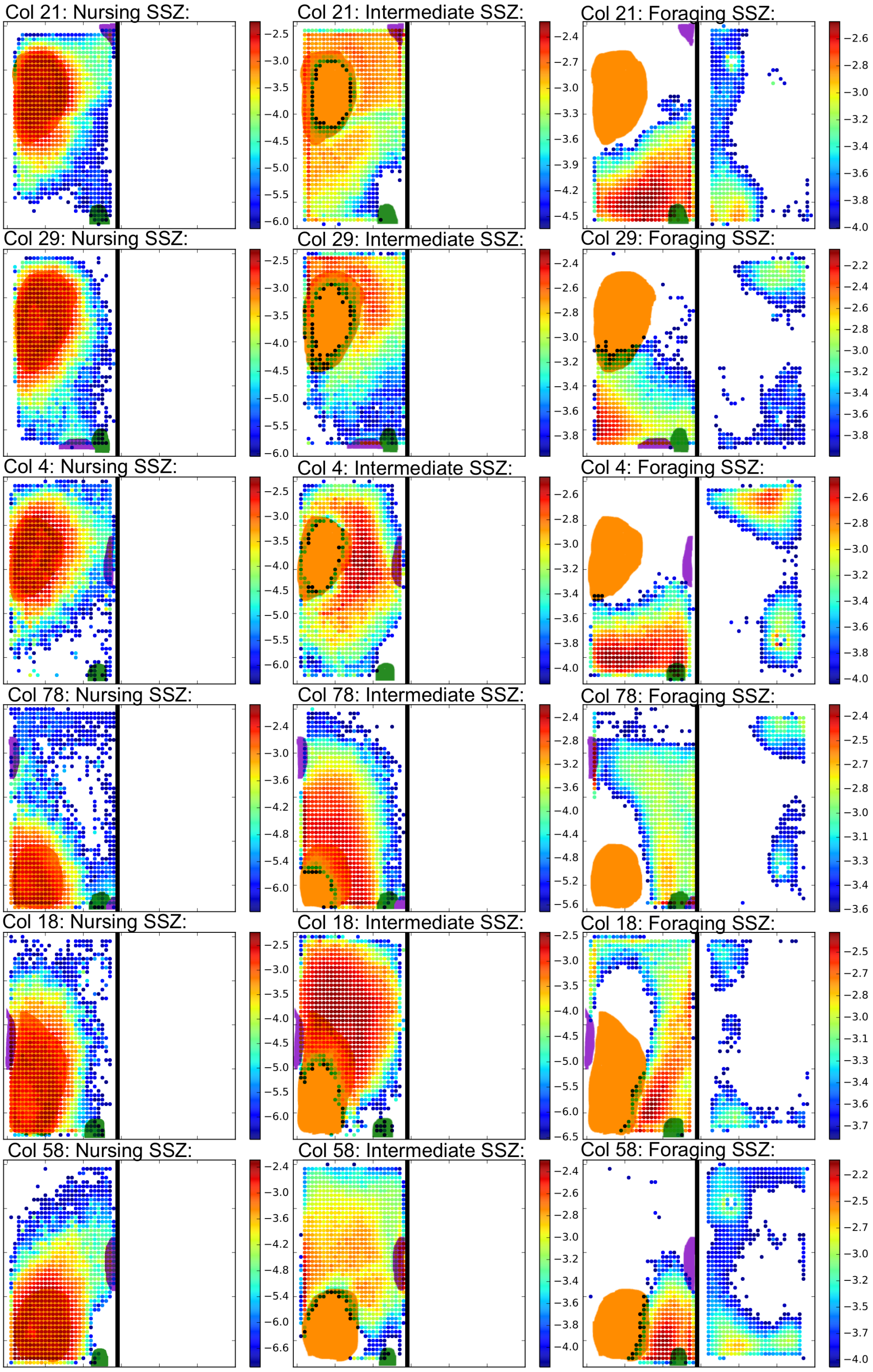

FIGURE 2.3: **Spatial segregation zones (SSZs).** For each colony and each type of SSZ, the SSZ is represented as a heatmap that shows the probability to be at each location of the nest (left of the thick black vertical line) and the foraging arena (right of the thick black vertical line). For clarity, only the top 1000 locations are represented and the color scale is in log (base 10) scale. For each panel, the heatmap of the SSZ is overlaid with visual annotations (Mersch et al., 2013b) of the brood pile (uniform orange zone), rubbish pile(s) (uniform purple zone[s]) and a highlight of the nest entrance (uniform green zone) of the colony on days 5 to 7 (see Materials and methods section 2.5.1 and Fig. 2.8 and 2.6).

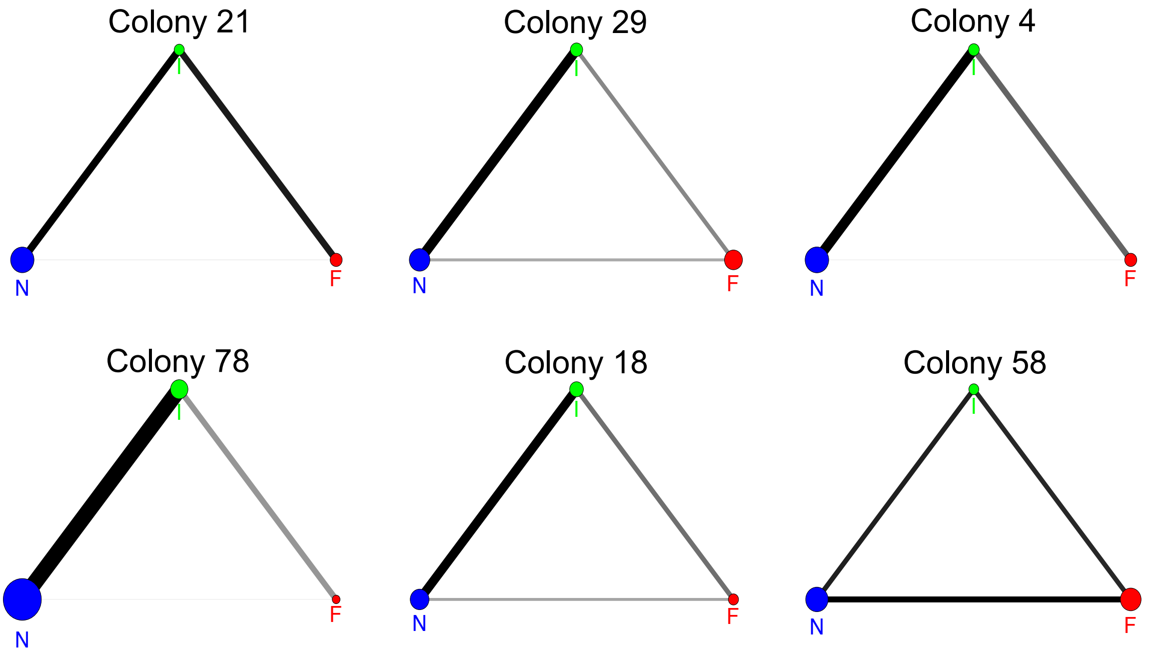

FIGURE 2.4: **Graphical network representation of the overlap values** $O_{z_1z_2} = \sum_x \theta_{z_1}(x)\,\theta_{z_2}(x)\,(z_1, z_2 = F, I, N; O_{z_1z_2} = O_{z_2z_1})$. Each node of these networks represents one of the three SSZs. The size of each node is proportional to the *size of the SSZ*, defined as the value of the overlap of a SSZ with itself ($O_{NN}, O_{II} \& O_{FF}$). The width and darkness of each edge are proportional to the value of the overlap between the two different SSZs ($O_{NI}, O_{IF} \& O_{FN}$) represented by the two nodes linked by this edge.

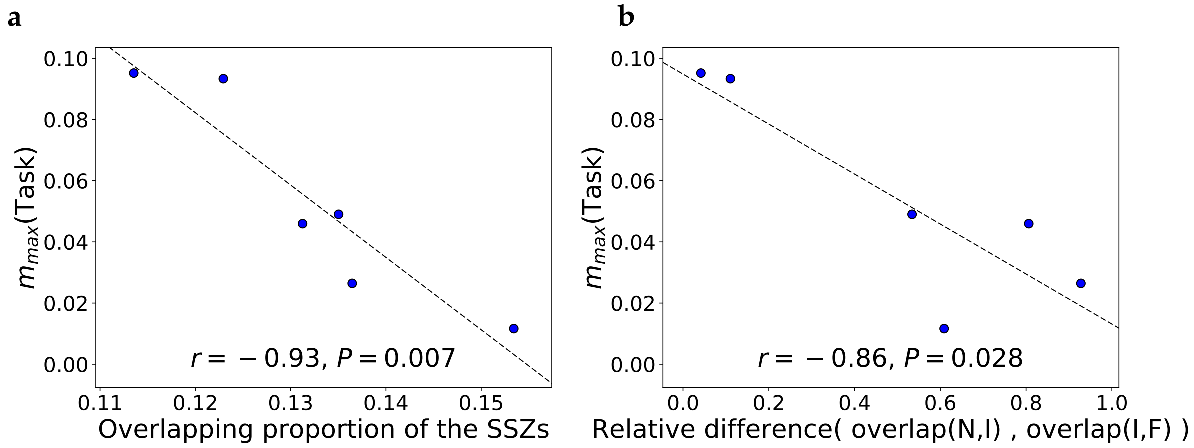

FIGURE 2.5: **Relation between the task dynamics of the workers (individual level) and the spatial segregation (colony level).** Each point represents a different colony. r is the Pearson correlation coefficient and is followed by its p-value (P). (**a**) Correlation between the expected maximum task specialization rate $m_{max}(Task)$ and the overlapping proportion of the SSZs (O_{all}; see Materials and methods section 2.5.6 for the mathematical definition). (**b**) Correlation between $m_{max}(Task)$ and the relative difference between the nursing-intermediate overlap (O_{NI}) and the intermediate-foraging overlap (O_{IF}). See Materials and methods section 2.5.7 for the mathematical definition of this relative difference.

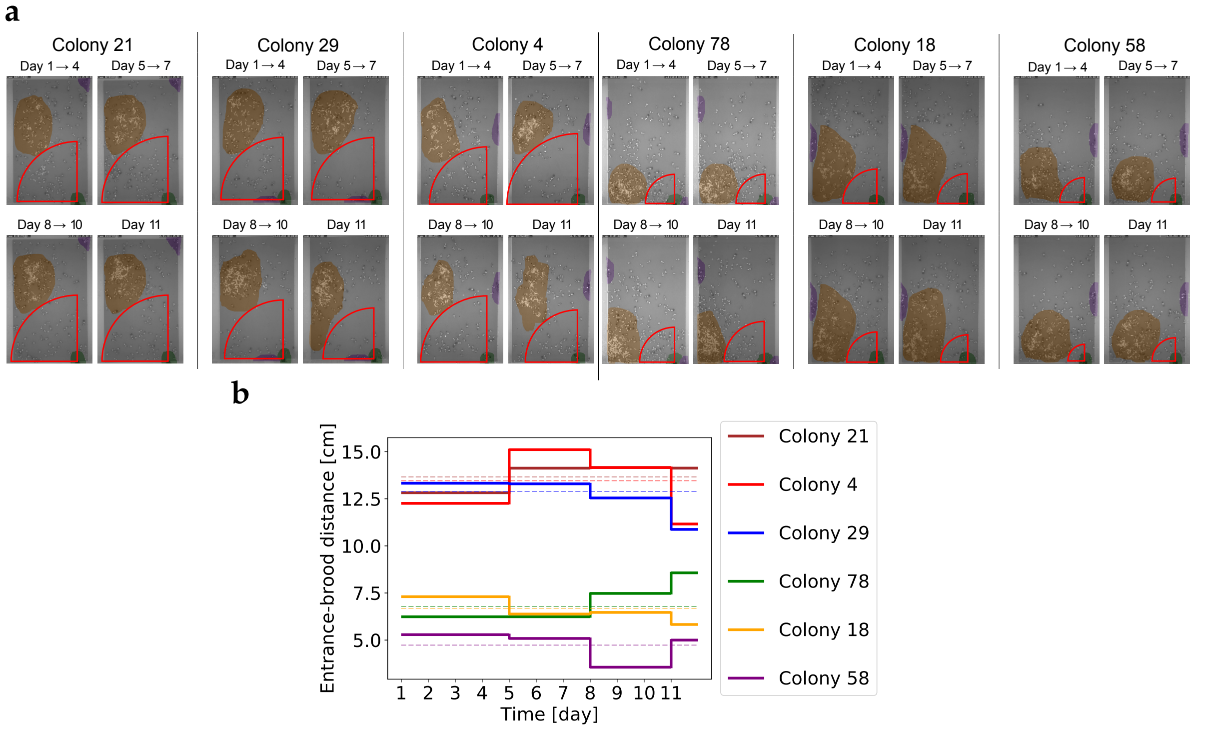

FIGURE 2.6: **Variation over time of the entrance-brood distance.** (**a**): Orange: brood pile, purple: rubbish pile. Green: highlight of the nest entrance. In red: our measurement of the entrance-brood distance. For more details, see Materials and methods section 2.5.3. (**b**): Each colored solid line represents the entrance-brood distance as a function of time for a different colony, the corresponding dashed line its average value over the 11 days.

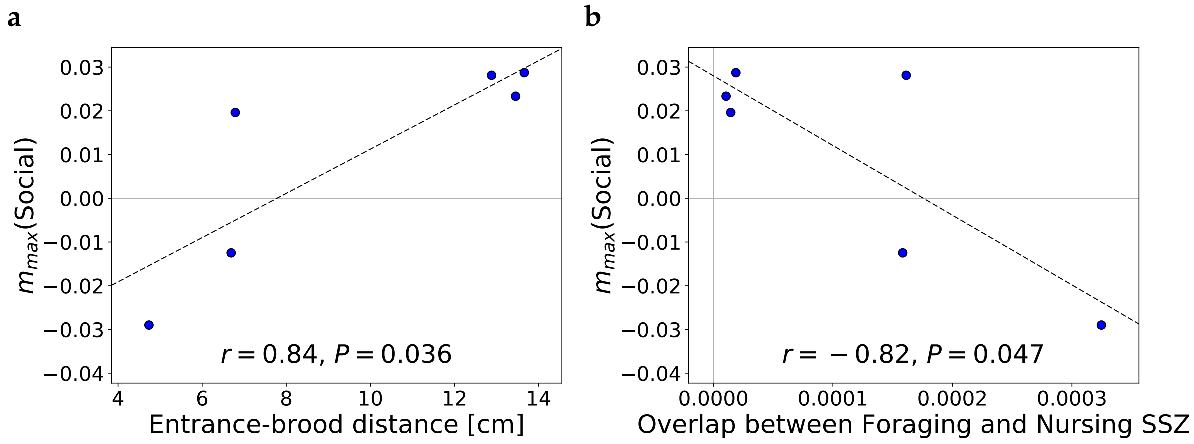

FIGURE 2.7: **Relation between the social dynamics of workers (individual level) and two colony-level properties: entrance-brood distance or foraging-nursing SSZs overlap.** Each point represents a different colony. r is the Pearson correlation coefficient and is followed by its p-value (P). (**a**): Correlation between the average entrance-brood distance and the expected maximum social maturation rate $m_{max}(Social)$. (**b**): Correlation between the overlap between Foraging and Nursing SSZs (O_{FN}) and $m_{max}(Social)$.

2.3 Discussion

In this chapter, we asked how individual-level properties, such as task specialization, social interactions and their dynamics, are related to each other and, through self-organization, to colony-level properties, such as the entrance-brood distance and the spatial segregation of the ants.

Interestingly, the spatial segregation revealed that the less the three SSZs overlapped, the faster were the task transitions from nursing to foraging. Therefore, when the SSZs are well-mixed (high overlap), the transition from nursing to foraging is slower than when the SSZs are segregated (low overlap). This could be due to the stimuli to perform a task in each SSZ being more mixed with one another when the SSZs are well-mixed, leading to a lowered stimulus perception (Bonabeau et al., 1996; McDonald and Topoff, 1985; Richardson et al., 2011). Mechanistically, as different SSZs are each recognized by the ants through a different chemical "road-sign" (Heyman et al., 2017), more overlapping (and mixed) SSZs could lead to more mixed chemical road signs, leading to a lowered stimulus perception. Overall, spatial segregation, by increasing stimulus perception, could accelerate task transitions, which in turn could enhance efficiency. Alternatively, the ants could be actively regulating their spatial segregation and thus the overlaps of the SSZs would be a correlate of the current regulation level. In order to segregate between those two alternative explanations, one would need to perform manipulative experiments where spatial segregation of the ants could be artificially controlled (for more detail on the experimental design see Perspectives p. 81). If such a treatment results in a significant acceleration of task transitions compared to control, we could conclude that it is increased spatial segregation that leads to accelerated task transition. If the treatment does not results in a significant acceleration of task transitions compared to control, the correlation we observe between task transition speed and spatial segregation could be the result of the ants actively regulating their spatial segregation or another common factor.

Our analysis of the spatial segregation further showed that the overlap between the foraging and the nursing SSZs was lower than the overlaps of both SSZs with the intermediate SSZ for most colonies (five out of six). Therefore, the SSZ of the intermediate group can be seen as a link between the nursing and the foraging SSZs. Furthermore, when this link was more balanced, i.e. when intermediate workers used the two other SSZs more equally, transitions from nursing to foraging were faster. This result highlights the importance of the SSZ of the intermediate group as a (balanced) link between the nursing and the foraging SSZs for regulating temporal polyethism.

Although the task specialization and the social maturity of individual ants in each colony were positively correlated and all colonies followed the predicted (Hölldobler and Wilson, 1990; Lenoir, 1979; Mersch et al., 2013b; Robinson, 1992; Seeley, 1982; Wilson, 1976) nurse to forager task dynamics, two colonies followed the inverse social dynamics from the forager social group to the nurse social group. Interestingly, this difference in individual-level dynamic properties could be explained by colony-level (relatively) static properties: the entrance-brood distance and the spatial segregation. The expected maximum social maturation rate was positively correlated with the nest entrance-brood pile distance and negatively correlated with the foraging-nursing SSZs overlap. Therefore, when the entrance-brood distance is short and the nursing-foraging SSZs overlap is high, the ants that interact as much with the nurse and the forager social group (i.e. with intermediate social maturity), are interacting less and less with the forager social group and more and more with the nurse social group (i.e. decreasing their social maturity), perhaps in order to enhance the protection of the brood, queen and nurses, which are closer to the nest entrance, from the diseases potentially brought back by the foragers. Alternatively, it could also be a means to regulate food flow from foragers to the brood and queen, or cuticular hydrocarbons exchange, or a consequence of some spatial rearrangements.

Overall our results highlight the link between individual-level dynamic properties (here, task and social dynamics) and colony-level structures (here, the entrance-brood distance and the spatial segregation of the ants), therefore revealing parts of the workings of self-organization.

2.4 Individual contributions

RB, under the supervision of DM and LK, did the analysis and wrote the chapter. DM, AC and LK provided the dataset (Mersch et al., 2013b) used for this analysis. MK, MG and PT modified their method from Kafsi et al. (2016) to create the SSZ extraction method used here and applied it on the dataset.

2.5 Materials and methods

2.5.1 Task specialization index

We tracked changes in individual task preference over time by calculating, for each ant, an index of task specialization that quantifies the number of visits to the brood pile and the foraging arena. The brood pile is the area in the nest in which the brood (larvae, eggs, pupae) is located. To obtain the location of the brood pile, we used visual annotation done by Mersch et al. (2013b). To account for the movement of the brood pile, Mersch et al. (2013b) split the 11 days of the experiment into four periods: days

1 to 4, days 5 to 7, days 8 to 10 and day 11. For each of those periods, the brood pile, shown in orange on Fig. 2.8 was visually annotated such that ants that are involved with brood at any time during the given period are detected inside the brood pile. The foraging arena was the box of the two-box tracking system, which contained food and water sources.

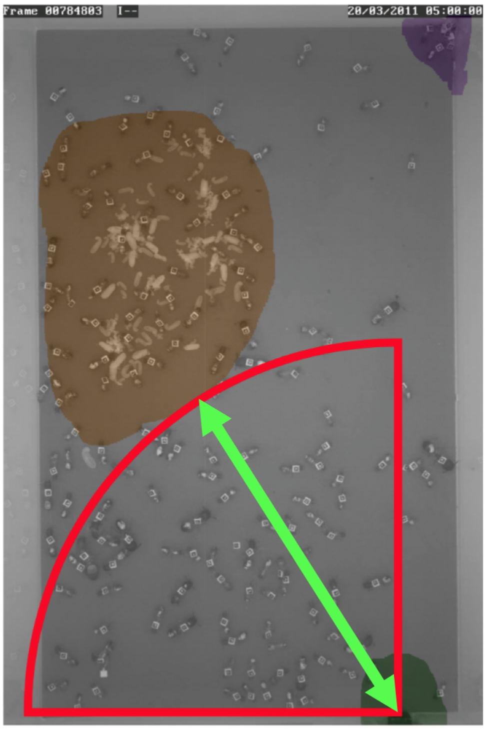

FIGURE 2.8: **Visual definition of the brood pile (Mersch et al., 2013b) and measurement of the entrance-brood distance** of colony 21 between days 5 and 7 of the dataset: Orange zone: brood pile, purple zone: rubbish pile. Green zone: highlight of the nest entrance. Green arrow: entrance-brood distance. The red arc of a circle was used to measure the entrance-brood distance. This arc of circle is centered at the nest entrance and has a radius such that it is just tangent to the orange zone.

We define an ant's task specialization index $T(i,t)$ as the number of visits it makes to the foraging arena relative to the total number of visits it makes to the brood pile and the foraging arena. If on day t, ant i makes $N_B(i,t)$ visits to the brood pile, and $N_F(i,t)$ visits to the foraging arena, the *task specialization* index is mathematically defined as:

$$T(i,t) = \frac{N_F(i,t)}{N_F(i,t) + N_B(i,t)}; T(i,t) = 0.5 \text{ if } N_F(i,t) = N_B(i,t) = 0 \tag{2.1}$$

We devised the index of task specialization $T(i,t)$ such that, similarly to the social maturity index $S(i,t)$, it is continuous and varies between 0 and 1 depending on the level of task preference between foraging and brood care. Ants with $T(i,t) = 0$ did a least one visit to the brood pile and no visit to the foraging arena on day t. Hence, a task specialization of 0 indicates that the ant was a nurse specialist. Ants with $T(i,t) = 1$ did a least one visit to the foraging arena and no visit to the brood pile. Thus, a task specialization of 1 indicates that the ant was a forager specialist. Ants with $T(i,t) = 0.5$ did exactly as many of visits to the foraging arena than to the brood pile (whether this number is zero or not) on day t. Thus, a task specialization of 0.5 indicates that the ant was exactly in between a nurse and a forager specialist. In addition, almost any values of $T(i,t)$ in between 0 and 1 are possible and the closer the value is to 0 the more the ant is specialized in nursing, the closer the value is to 1 the more the ant is specialized in foraging.

It has to be noted that our measure of task specialization $T(i,t)$ was more coarse-grained than our measure of social maturity, especially for ants that did not leave the nest. Indeed, from the mathematical definition of $T(i,t)$ above (Equation 2.1), we see that ants that did not leave the nest but visited the brood pile at least once all have $T(i,t) = 0$, and those ants could have variations in their interactions with ants within the nest which would result in variations in social maturity (as can be seen on on Fig. 2.2).

2.5.2 Dynamics of task specialization and social maturity

To understand the link between the dynamics of task specialization and social maturity, we first analyzed them separately. Similarly to Chapter 1 for social maturity, we performed the following three steps, but for both task specialization and social maturity separately. First, we performed for each ant a linear regression of the social maturity (or task specialization) upon time for all 11 days. Second, we plotted the scatter plot of the slopes of those linear regression lines as a function of the 11-day mean social maturity (or task specialization). Third, we fitted a hill function to this scatter plot to obtain the unique parameter characterizing the sigmoidal curve of social maturation (or task specialization): $m_{max}(Social)$ corresponding to the expected maximum social maturation rate (or $m_{max}(Task)$ corresponding to the expected maximum task specialization rate). The sign of $m_{max}(Social)$ (or $m_{max}(Task)$) gives the direction of the transition. If $m_{max}(Social) > 0$, ants change from the nurse social group to the forager social group, by interacting more and more with foragers and less and less with nurses. Or, if $m_{max}(Task) > 0$, ants change from the nurse task group to the forager task group, by doing more and more visits to the foraging arena and less and less to the brood pile. If $m_{max}(Social) < 0$, ants change from the forager social group to the nurse social group, by interacting more and more with nurses and less and less with foragers. Or, if $m_{max}(Task) < 0$, ants change from the forager task group to the nurse task group, by doing more and more visits to the brood pile and less and less to the foraging arena. The p-value associated with m_{max} tells us whether m_{max} is significantly positive or negative and therefore whether the nurse to forager (if $m_{max} > 0$) or forager to nurse (if $m_{max} < 0$) transition can be considered significant. The fit of the hill function was done with a non-linear least-squares model fitted using the 'nls' function of the 'stats' library in 'R'. We then used the 'summary.nls' function of the same library to extract the estimated value of m_{max}, its standard error, t-statistic and corresponding (two-sided) p-value.

In Chapter 1, the linear regression of the social maturation was done upon the first seven days of tracking to keep four days for the prediction step. In this chapter, to maximize the amount of data, we used all 11 days for both the social dynamics and the task dynamics.

2.5.3 Entrance-brood distance

To measure the entrance-brood distance (Fig. 2.8), which varied over time and across colonies, we traced an arc of a circle (shown in red on Fig. 2.8), that is centered at the nest entrance and with a radius such that it is just tangent to the brood pile zone (orange zone on Fig. 2.8). We chose to measure the entrance-brood distance because we are interested in the nurse to forager transition and this distance is the shortest distance between the single point of entry of the foragers into the nest, the nest entrance, and the closest limit of the brood pile zone and quantifies the spatial separation between the nurse and the forager task zones.

2.5.4 Spatial segregation zones (SSZs)

To identify and count the SSZs purely based on the spatial distributions of all ants, and assign each worker to its most likely SSZ, we used a slightly modified version of the machine learning method devised in Kafsi et al. (2016). In the original method of Kafsi et al. (2016), both the spatial distributions and the activity level of all ants were used. Because here we are interested in the SSZs independently of the level of activity of the ants, this modified version of the method only used the spatial distributions of all ants. This modified version of the method models the probability $p(X_i(t) = x)$ that ant i spatial location at time t is equal to a given location x, as a time-dependent mixture of K multinomial distributions $\theta_z(x), z = 1, 2, ..., K$, each representing a SSZ as a probability distribution of location x:

$$p(X_i(t) = x) = \sum_{z=1}^{K} p(x|z)p(z|i,t) = \sum_{z=1}^{K} \theta_z(x)\pi_i(t,z)$$

Where the K multinomial distributions $\theta_z(x)$ each represent the probability $p(x|z)$ that an ant with SSZ z is at the location x, and the mixture coefficient $\pi_i(t,z)$ represents the probability $p(z|i,t)$ that ant i at time t has SSZ z. In other words, the probability that an ant is at a given place a given time is modeled as a linear combination of K SSZs, where each SSZ (collective part of the model) is modeled as probability distribution of locations. The method then finds the parameters $\{\theta_z(x), \pi_i(t,z)\}$ of this model that maximizes the probabilities of the observed data using *Expectation Maximization* (*EM*) (Bishop, 2006).

One of the great advantages of this method is that it does not make any assumption on the size and number K of SSZs, allowing us to automatically identify and count the SSZ $\theta_z(x)$ purely based on the spatial distributions of all ants, and then assign to each worker a probability $\pi_i(t,z)$ to belong to each SSZ at time t. In addition, the representation of the SSZ as a probability distribution allows a much more precise vision of it than if it is simply represented as an area.

2.5.5 Overlap between SSZs

To compare the spatial segregation to the dynamics of task specialization and social maturation, we summarized the spatial segregation by the six *overlap values* between SSZs. Those values are defined as follows: the overlap value $O_{z\tilde{z}}$ between SSZ z and SSZ $\tilde{z}$, where $\tilde{z}, z = F$(Foraging SSZ), I(Intermediate SSZ), N(Nursing SSZ), is given by:

$$O_{z\tilde{z}} = \sum_x \theta_z(x)\theta_{\tilde{z}}(x) = \sum_x p(x|z)p(x|\tilde{z}); O_{z\tilde{z}} = O_{\tilde{z}z} \, ,$$

where the overlap value $O_{z\tilde{z}}$ between SSZ z and SSZ $\tilde{z}$ represents the extent to which z spatially overlaps with $\tilde{z}$. The value of $O_{z\tilde{z}}$ is proportional to the spatial overlap between z and $\tilde{z}$.

Those six numbers (O_{NI},O_{IF},O_{FN},O_{NN},O_{II},O_{FF}) can be graphically represented as a three-node network where each node represents one of the three SSZs and its overlap value with itself (O_{NN},O_{II} and O_{FF}) and each undirected edge represents the overlap value between the two different SSZs it links (O_{NI},O_{IF} and O_{FN}; see Fig. 2.4).

2.5.6 Overlapping proportion of the SSZs

To summarize further the six overlap values into one single number (per colony), we computed O_{all} the *overlapping proportion of the SSZs*. O_{all} is the proportion of the area of all the SSZs that overlap with at least another one. It was computed with the following formula:

$$O_{all} = \frac{\sum \text{edge weights of Fig. 2.4}}{\sum \text{node sizes of Fig. 2.4}} = \frac{O_{NI} + O_{IF} + O_{FN}}{O_{NN} + O_{II} + O_{FF}}$$

A value $O_{all} = 0$ means that the three SSZs are not at all overlapping with each other and that the three SSZs are hence disjoint. A value $O_{all} = 1$ means that the three SSZs are maximally and fully overlapping and that the three SSZs are thus coincident.

2.5.7 Balance of the overlap between SSZs

To quantify the balance of the overlap of the intermediate SSZ with the two other SSZs (nursing and foraging SSZs), we use the relative difference between O_{NI} and O_{IF}:

$$\frac{O_{NI} - O_{IF}}{mean\left(O_{NI}, O_{IF}\right)} = 2 \cdot \frac{O_{NI} - O_{IF}}{O_{NI} + O_{IF}}$$

The smaller this relative difference the more balanced is the overlap of the intermediate SSZ with the nursing SSZ and the foraging SSZ.

2.6 Appendix

2.6.1 Within colony change of brood position and social dynamics

We showed that between colonies $m_{max}(Social)$ (the expected maximum social maturation rate) was significantly positively correlated with the entrance-brood distance (Pearson's $r = 0.84$, $P = 0.036$; Fig. 2.7a). We see that within each colony the correlations were also positive, but because we lost statistical power, those positive correlations are not significant anymore ($P > 0.238$; Fig. 2.9).

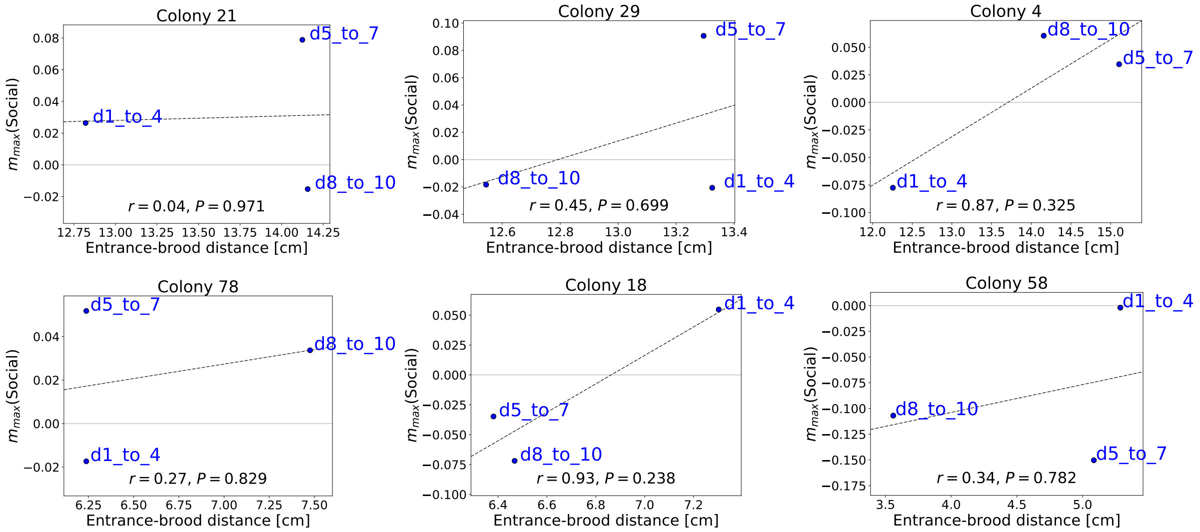

FIGURE 2.9: **Within colony change of brood position and social dynamics.** For each colony, correlation between the entrance-brood distance and the expected maximum social maturation rate m_{max}(social) at different time frames. Each panel shows a different colony. Each point shows a different time frame: days 1 to 4 ('d1_to_4'), days 5 to 7 ('d5_to_7') and days 8 to 10 ('d8_to_10'). r is the Pearson correlation coefficient and is followed by its p-value (P).

Chapter 3

Behavioral resilience to targeted workforce removal in ants

Collaborators on this chapter:

Raphaël Braunschweig[1]; Danielle Mersch[1]; Alessandro Crespi; Laurent Keller

3.1 Introduction

Chapter 1 and 2 focused on social maturation and task specialization (collectively referred to as *behavioral trajectory*) of workers of an unperturbed colony, which in general change from nursing to foraging as they age (Hölldobler and Wilson, 1990; Lenoir, 1979; Mersch et al., 2013b; Robinson, 1992; Seeley, 1982; Wilson, 1976). However, ant colonies are often exposed to external perturbations that can damage them. For example, major floods could cause a loss of foragers (Avril et al., 2016; Purcell et al., 2014) which may lead to a decrease in food supply for the colony, thereby weakening the colony. Therefore, if external perturbations lead to a disproportionate loss of workers specialized in a specific task, the colony could be particularly weakened. Hence, it

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[1] These collaborators contributed equally to this work.

has been hypothesized that the surviving workers should exhibit behavioral flexibility (Calabi and Traniello, 1989a; Franks and Tofts, 1994; Gordon, 1996) to compensate loss of a specific workforce. Such flexibility is ubiquitous in complex biological networks. For example, gene-transcription networks compensate for gene knockout by up-regulating transcription of duplicate genes (Kitano, 2004).

Surprisingly, it is still controversial if colonies can flexibly adjust to such perturbations through behavioral changes at the level of individual workers. The popular view is that social insects adopt flexible behavioral strategies (Gordon, 1996). However, this view is mainly based on theoretical models such as *Foraging for work* (Franks and Tofts, 1994; Tofts, 1993; Tofts and Franks, 1992) or network models of task allocation (Gordon et al., 1992; Pacala et al., 1996). In *Foraging for work*, unemployed workers actively seek work to perform and thus would perform any new task needed after a perturbation. In network models, workers communicate, through social interactions, information about task need. Clear experimental evidence of such flexibility is mainly found in bees, where workers compensated for lost workforce (Bloch and Robinson, 2001; Huang and Robinson, 1992; Huang and Robinson, 1996; Lindauer, 1952; Winston and Fergusson, 1985). In those bee studies, removal of foragers induces nurses to switch to foraging and removal of nurses induces foragers to switch to nursing. In ants, evidence indicates that the amount of individual behavioral flexibility in response to specific workforce loss varies among species. Specifically, in the leaf-cutter ant *Atta cephalotes*, removing 90% of the physical caste usually most involved in cutting leaves triggered workers from other physical castes to cut leaves instead (Wilson, 1983). For minors of the dimorphic ant *Pheidole dentata*, old minors, in colonies without young minors, performed, in addition to their usual foraging tasks, the nursing tasks usually performed by young minors (Calabi and Traniello, 1989b). Moreover, young minors, in colonies without old minors, performed, in addition to their usual nursing tasks, the foraging tasks. In the three dimorphic ant species *Pheidole guilelmimueller*, *Pheidole pubiventri* and *Pheidole megacephal*, majors took over the typical tasks of removed minors, when all minors were removed (Wilson, 1984). In the Florida harvester ant *Pogonomyrmex badius*, removing 50% of the foragers did not induce other workers to compensate for the lost workforce (Kwapich and Tschinkel, 2013). No precocious foraging was observed, the removed foragers were not replaced and the number of brood items decreased. Overall, evidence of individual behavioral flexibility in response to specific workforce loss has been found in five studies each on a different ant species: *A. cephalotes* (removal of 90% of a caste), *P. dentata* (removal of 100% of a caste), *P. guilelmimueller*, *P. pubiventri* and *P. megacephal* (removal of 100% of a caste) and evidence of a lack of such flexibility has been found in one ant study: *P. badius* (removal of 50% of a caste). From those studies, it seems therefore that behavioral flexibility in ants could be triggered when most of a caste is removed (90%-100%) but not when 50% of a caste is removed. In all of those studies, the social interactions and detailed behavior of all ants of the colonies at all times were not tracked. However, to understand how a colony responses to external perturbation and as social interactions contribute to the regulation of task specialization (Chapter 2, Greene and Gordon, 2003; Pless et al., 2015; Razin et al., 2013; Robinson et al., 2009b, Mersch, 2016), such tracking is necessary.

To further widen the number of ant species on which removal experiments are performed, we chose the *Camponotus fellah* ant species. We chose this species because it could be easily tracked in our tracking system (Mersch et al., 2013b) and because we already performed a detailed analysis of the social maturation and task specialization of unperturbed colonies (see Chapter 1 and 2).

To investigate the resilience of colonies of the ant *C. fellah* to the loss of some specific group of workers, we performed three types of targeted removal: a forager removal, a nurse removal and a control removal. We used our tracking system (Mersch et al., 2013b) to constantly monitor the positions, the task specialization and the social interactions of all ants of the colony before and after the removals. We then asked whether the remaining workers deviate from their task specialization trajectory to compensate for the lost workforce.

Because social interactions contribute to the regulation of task specialization (Chapter 2, Greene and Gordon, 2003; Pless et al., 2015; Razin et al., 2013; Robinson et al., 2009b, Mersch, 2016), we further asked how the social network rewires after the worker removal. In addition, as social groups in the social network are associated with tasks (Chapter 2, Mersch et al., 2013b), we asked whether the social groups were maintained after the removal.

3.2 Results

3.2.1 Before removal

We tracked all individuals over seven days to build the daily social networks, determined the social maturity index (see Chapter 1) of each individual every day and identified which individuals visited the foraging box and for how long. During the seven days before removal, the mean (± standard deviation) percentage of ants of the colonies in the foraging box was $8.6 \pm 2.2\%$ (percentages in the five colonies to which the forager removal was subsequently applied [mean ± standard deviation $=$ $8.0 \pm 3.0\%$]: 11.8%, 4.4%, 7.8%, 6%, 9.7%; percentages in the five colonies to which the nurse removal was subsequently applied [mean ± standard deviation $= 9.8 \pm 1.7\%$]: 11.1%, 7.9%, 8.5%, 11.9%, 9.4%; percentages in the five colonies to which the control removal was subsequently applied [mean ± standard deviation $= 8.2 \pm 1.8\%$]: 6.6%, 10.5%, 7.2%, 6.8%, 9.8%).

In each colony, we removed 25% of the workforce based on their social maturity on day seven. We had three treatments, each with five colonies. In the first treatment, referred to as *forager removal*, we removed the 25% of workers most embedded in the forager social group, i.e. with the highest social maturity, resulting in the removal of $94.0 \pm 4.6\%$ (mean ± standard deviation) of the ants that visited the foraging box during the seven days before removal (percentages in the five colonies to which the forager removal was applied: 87.2%, 97.5%, 93.8%, 98.9%, 92.6%). In the second treatment, referred to as *nurse removal*, we removed the 25% of workers most embedded in the nurse social group, i.e. with the lowest social maturity, resulting in the removal of $3.1 \pm 2.4\%$ of the ants that visited the foraging box during the seven days before removal (percentages in the five colonies to which the nurse removal was applied: 1.7%, 3.8%, 3.5%, 0%, 6.4%). In the third treatment, referred to as *control removal*, we removed again 25% of the workers, but to preserve the ratios between the nurse and the forager social group, we ranked all ants according to their social maturity and removed every 4th ant, resulting in the removal of $44.1 \pm 18.3\%$ of the ants that visited the foraging box during the seven days before removal (percentages in the five colonies to which the control removal was applied: 28.2%, 33.3%, 60.6%, 67.2%, 31.3%).

3.2.2 After removal

In each colony, we then tracked all remaining workers and the queen for another 13 days to assess whether colonies reallocate workers to compensate for the lost workforce.

3.2.2.1 Task specialization

If colonies flexibly adjust the development of the workforce to maintain a balance between the nursing and foraging roles, we predict that colonies where nurses are removed should reduce the rate at which workers transition to foraging, or even reverse the normal behavioral trajectories, to replace the lost nurses. Conversely, the forager removal should induce an increase of the rate at which workers transition to foraging, to replace the lost foragers. To test formally those predictions, we define the *foraging transition rate* as the average rate at which workers transition to the foraging group. We quantified the foraging transition rate as the daily change of the average proportion of ants in the foraging box every day before and after the removal. Finally, we tested whether the foraging transition rate depended on the 'period' (before or after removal) and the 'treatment' (Nurse removal, forager removal or control removal) using a linear mixed effect model. The effect of removal was similar in the forager removal and the control removal (interaction between 'period' and 'treatment' [forager vs. control removal] in the linear mixed effect model: $t_{36.93} = -0.662$, $P = 0.51$), and was similar in the nurse removal and the control removal (interaction between 'period' and 'treatment' [nurse vs. control removal] in the linear mixed effect model: $t_{36.93} = -0.540$, $P = 0.59$). The effect of removal was therefore similar in the three treatments, suggesting that ants do not compensate for the lost workforce in both the nurse removal and the forager removal. See Fig. 3.1 and Appendix: Table 3.1.

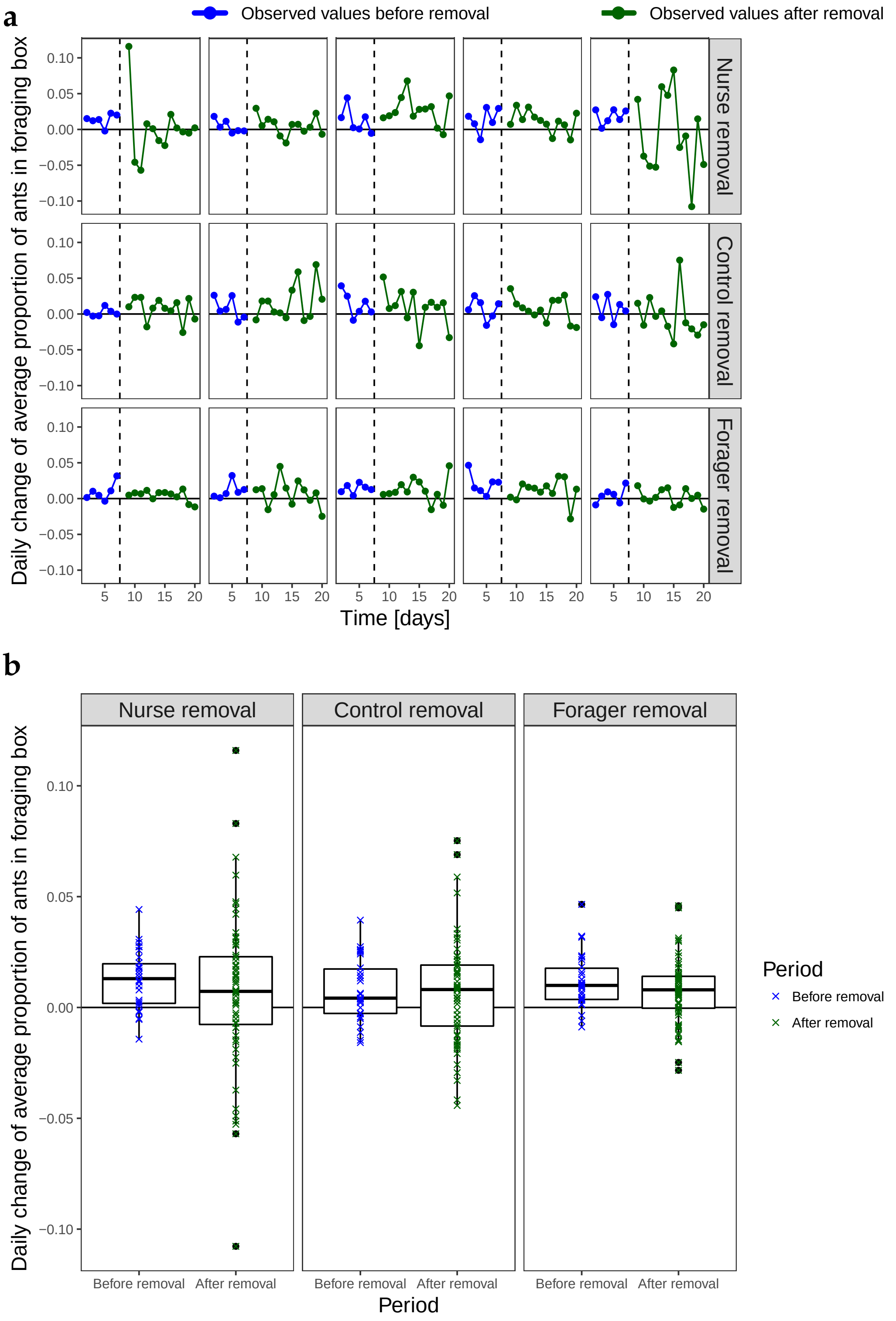


FIGURE 3.1: **Effect of the nurse removal, forager removal and control removal on the daily change of the average proportion of ants in the foraging box.** (**a**): Each panel represents a different colony with a given treatment (given by the panel row number) and a given replicate (given by the panel column number). (**b**): Boxplot for the fixed effects of the linear mixed effects model (see Appendix section 3.6.1 for the 'R' formula and the summary statistics table and see Materials and methods section 3.5.2.1 for more details).

3.2.2.2 Social network analysis

To measure the effect of removal on the social network of the remaining ants, we compared the observed networks after the removal to the network under the *null hypothesis* which assumes that the ants did not perform any active modification of their social interactions (i.e. *no active rewiring*) in response to the removal. The network under the null hypothesis was constructed by removing the ants (nodes) and all the social interactions they had (edges) from the network on the last day before removal (day 7). Because the comparisons were made between the observed networks after the removal and the null hypothesis (same ants removed but no active rewiring), the change of social interactions reported here are only among non-removed ants. For example, when foragers were removed it is the change of interactions between non-foragers and themselves that were reported.

3.2.2.2.1 Social network rewiring

To investigate how the social network rewires in response to the removal, we analyzed the effect of removal on three common network measures: the number of interaction partner of an ant (*degree*), the number of interactions per interacting ant pair (*weight*) and the number of interactions per ant (*strength*). For this analysis, we are interested in measuring those three network measures at steady state, or the closest to steady state we can get to. Before the removal, the best measure of a steady state is on day 7, because it is the longest since the previous perturbation (separating the tagged ants from the untagged ones and placing them in the tracking box). We compared this before-removal measure six days after a perturbation (with the null hypothesis applied to it) to its after-removal equivalent: the measure six days or more after the removal, also referred to as *long-term*. To measure what happened between the removal and the long term, we compared the day before the removal (with the null hypothesis applied to it) to the period between one and five days after the removal, also referred to as *mid-term*. To avoid measuring the effect of the state of alarm in which the ants were directly after the removals, the day directly following the removal was removed from the analysis.

Our analysis of the rewiring of the social network showed that, in the long term, the forager removal induced a significantly greater decrease (compared to the network under the null hypothesis) of the mean number of interaction partners per ant than the two other treatments ($P < 10^{-4}$; Fig. 3.2b and Appendix: Table 3.2b). In addition, in the long term, the forager removal induced a significantly smaller increase of the mean number of interactions per interacting ant pair than the two other treatments ($P < 10^{-3}$; Fig. 3.3b and Appendix: Table 3.3b). Finally, in the long term, the forager removal induced a significantly greater decrease of the mean number of interactions per ant than the two other treatments ($P < 10^{-3}$; Fig. 3.4b and Appendix: Table 3.4b). In the mid-term, no significant treatment differences could be seen ($P > 0.05$; Fig. 3.2a, 3.3a, 3.4a and Appendix: Table 3.2a, 3.3a, 3.4a). For more details on the statistical analysis used here, see Materials and methods section 3.5.2.2.1.

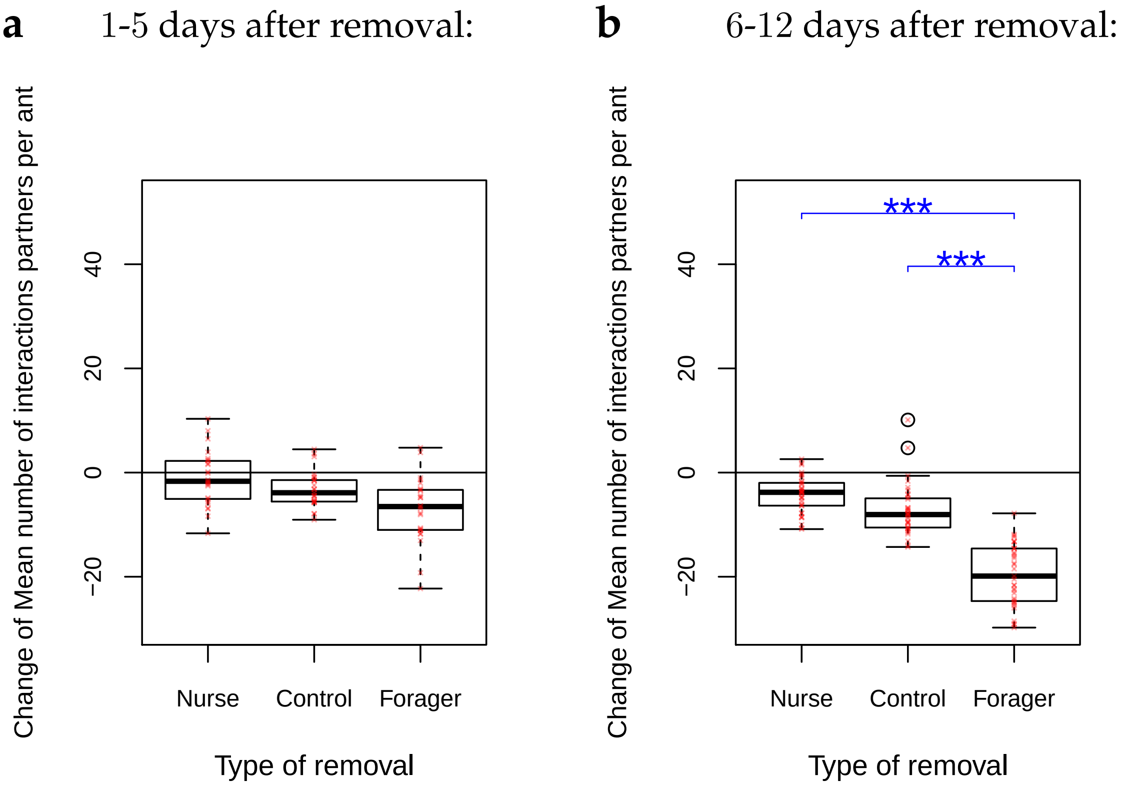


FIGURE 3.2: **Effect of removal (compared to null hypothesis) on the mean number of interactions partners per ant**. Boxplot showing the effect of 'treatment' on the change of the mean number of interactions partners per ant compared to null hypothesis, 1-5 days (**a**) and 6-12 days (**b**) after the removal. Results of the post-hoc comparison tests are shown with the following significance codes on the box plots: $*** = [P < 0.001]$, $** = [P < 0.01]$, $* = [P < 0.05]$. See Appendix section 3.6.2 for the 'R' formula and the summary statistics tables and see Materials and methods section 3.5.2.2 for more details.

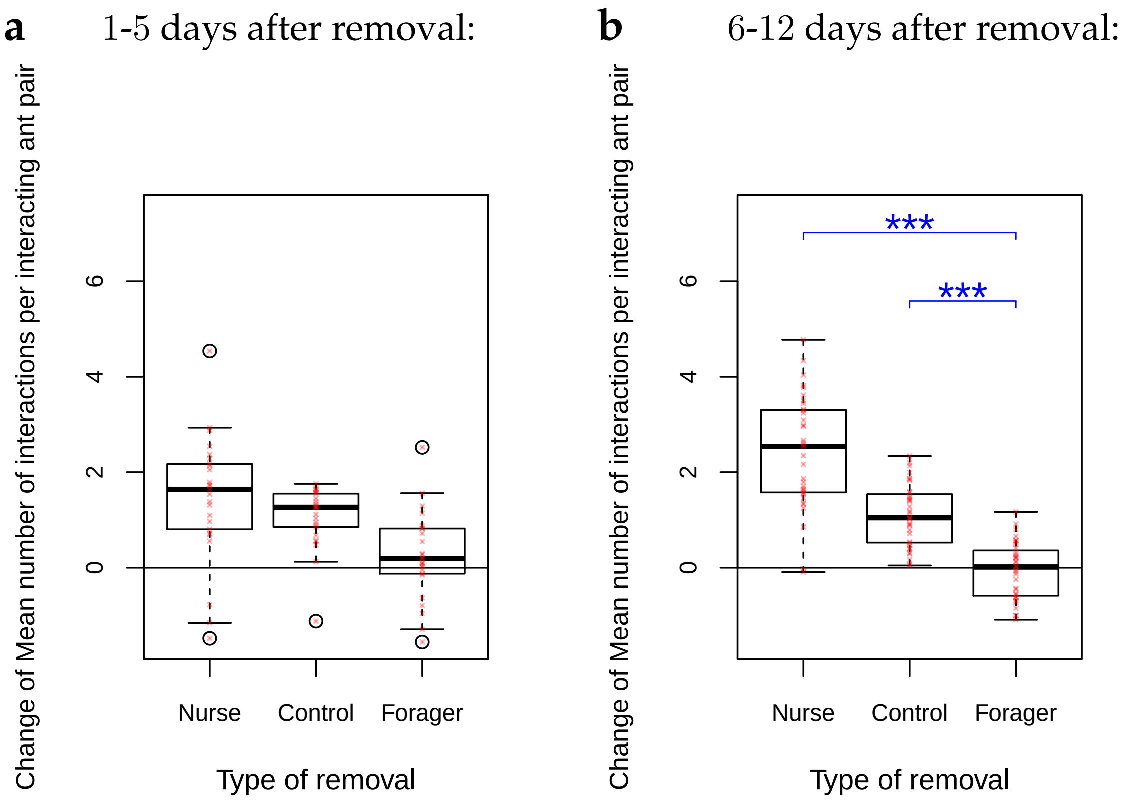


FIGURE 3.3: **Effect of removal (compared to null hypothesis) on the mean number of interactions per interacting ant pair**. Boxplot showing the effect of 'treatment' on the change of the mean number of interactions per interacting ant pair compared to null hypothesis, 1-5 days (**a**) and 6-12 days (**b**) after the removal. Results of the post-hoc comparison tests are shown with the following significance codes on the box plots: $* * * = [P < 0.001]$, $** = [P < 0.01]$, $* = [P < 0.05]$. See Appendix section 3.6.2 for the 'R' formula and the summary statistics tables and see Materials and methods section 3.5.2.2 for more details.

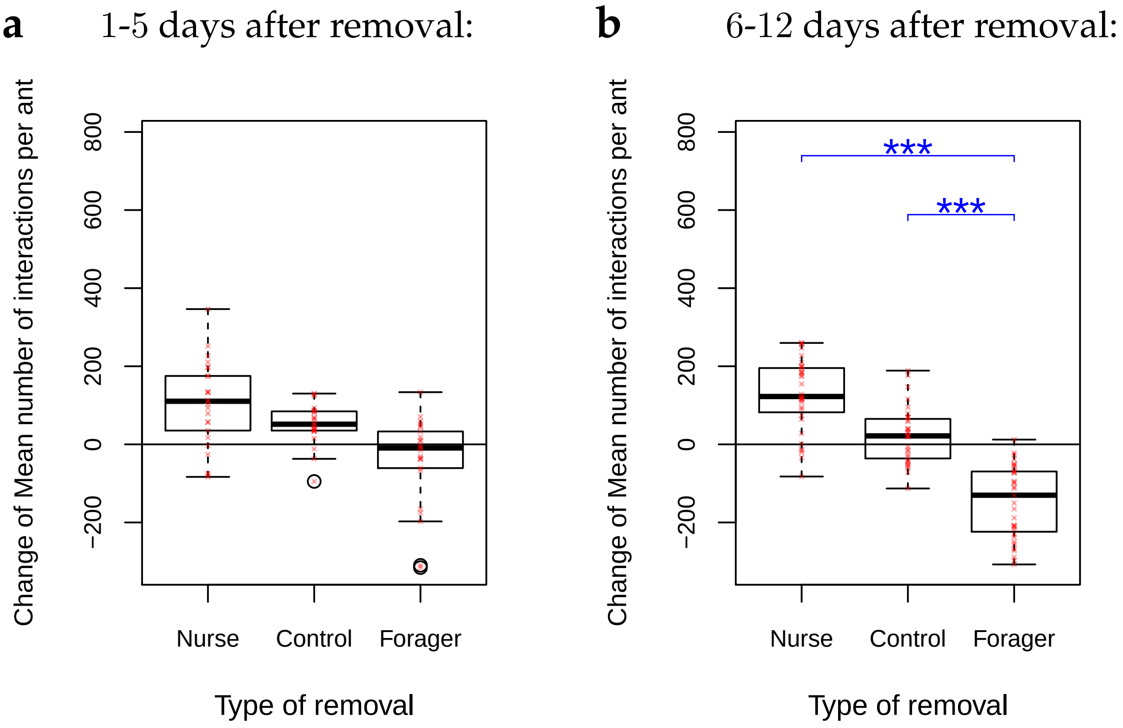


FIGURE 3.4: **Effect of removal (compared to null hypothesis) on the mean number of interactions per ant**. Boxplot showing the effect of 'treatment' on the change of the mean number of interactions per ant compared to null hypothesis, 1-5 days (**a**) and 6-12 days (**b**) after the removal. Results of the post-hoc comparison tests are shown with the following significance codes on the box plots: $*** = [P < 0.001]$, $** = [P < 0.01]$, $* = [P < 0.05]$. See Appendix section 3.6.2 for the 'R' formula and the summary statistics tables and see Materials and methods section 3.5.2.2 for more details.

3.2.2.2.2 Social groups

In all three treatments (nurse, forager and control removal) and in both the mid term (1 to 5 days after the removal) and the long-term (6 to 12 days after the removal), the proportion of *groupless ants* (ants that cannot be attributed significantly to any social group by the OLSOM algorithm; Lancichinetti et al., 2011) was not significantly different than predicted by the null hypothesis ($P > 0.22$, see Fig. 3.5 and Appendix: Table 3.5).

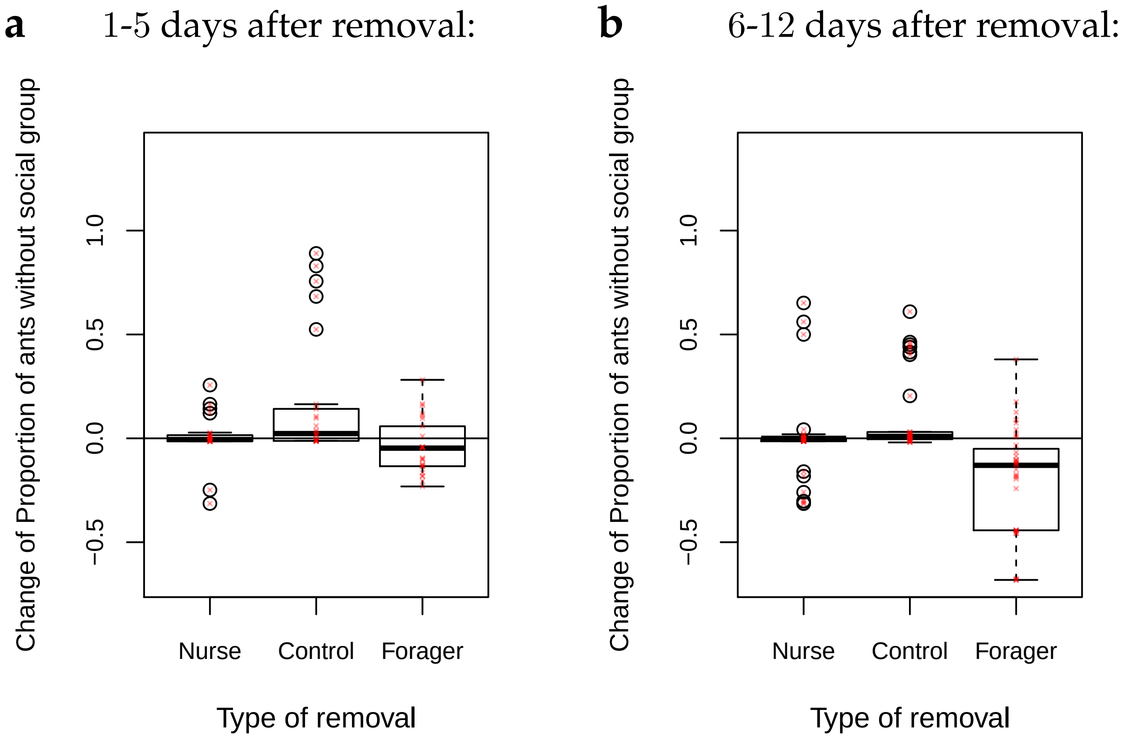


FIGURE 3.5: **Effect of removal (compared to null hypothesis) on the proportion of ants without social group**. Boxplot showing the effect of 'treatment' on the change of the proportion of ants without social group compared to null hypothesis, 1-5 days (**a**) and 6-12 days (**b**) after the removal. Results of the post-hoc comparison tests are shown with the following significance codes on the box plots: $*** = [P < 0.001]$, $** = [P < 0.01]$, $* = [P < 0.05]$. See Appendix section 3.6.2 for the 'R' formula and the summary statistics tables and see Materials and methods section 3.5.2.2 for more details.

Finally, in all three treatments (nurse, forager and control removal) and in both the mid term and the long term, OSLOM detected a number of groups not significantly different from the prediction of the null hypothesis ($P > 0.53$; Fig. 3.6 and Appendix:

Table 3.6).

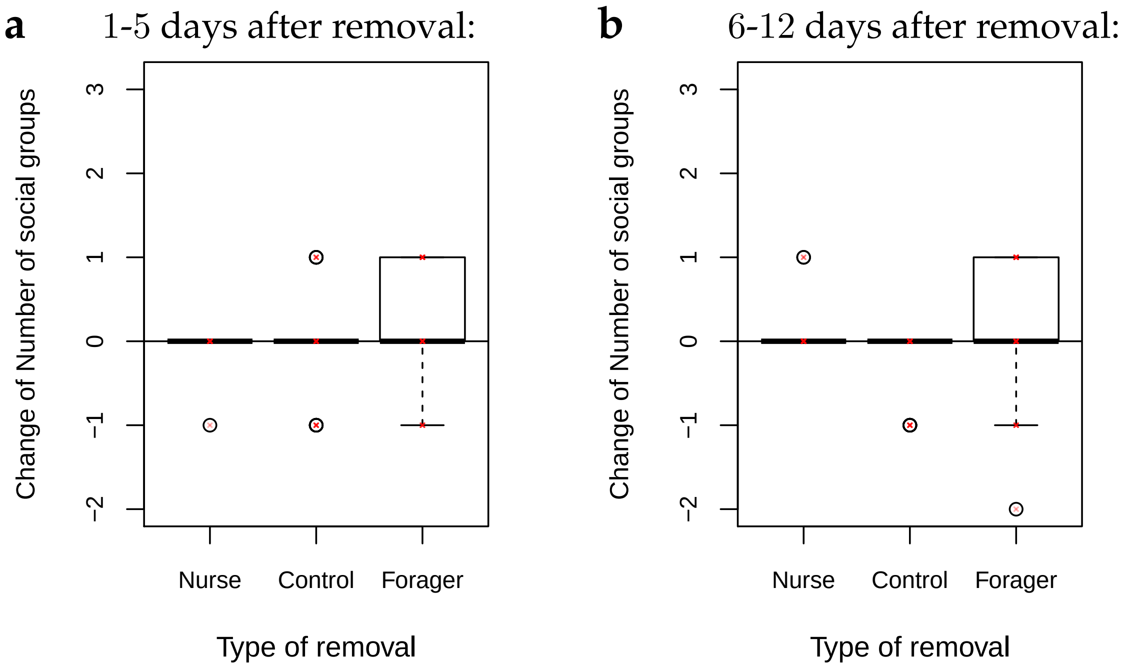


FIGURE 3.6: **Effect of removal (compared to null hypothesis) on the number of social groups**. Boxplot showing the effect of 'treatment' on the change of the number of social groups compared to null hypothesis, 1-5 days (**a**) and 6-12 days (**b**) after the removal. Results of the post-hoc comparison tests are shown with the following significance codes on the box plots: $*** = [P < 0.001]$, $** = [P < 0.01]$, $* = [P < 0.05]$. See Appendix section 3.6.2 for the 'R' formula and the summary statistics tables and see Materials and methods section 3.5.2.2 for more details.

3.3 Discussion

Our results show that *C. fellah* workers do not compensate for the lost of specific workforce, following both the nurse removal and the forager removal, suggesting an inability to allocate workers dynamically depending on the available workforce. Conversely, workers pursued their normal task specialization time line independently of treatment, suggesting that their task specialization time line is rigidly preprogramed rather than flexibly adjusting in response to perturbations. This is in contradiction with the popular view that social insects adopt flexible behavioral strategies (Gordon, 1996).

However, this view is mainly based on theoretical models. Evidence from removal experiments rather shows that, in ants, this flexibility varies among studies and species (Calabi and Traniello, 1989b; Wilson, 1983; Wilson, 1984; Kwapich and Tschinkel, 2013) and could so far be explained by the differences in designs. In those studies behavioral flexibility in ants was triggered when most (90%-100%) of a caste was removed in *A. cephalotes* (Wilson, 1983), *P. dentata* (Calabi and Traniello, 1989b), *P. guilelmimueller*, *P. pubiventri* and *P. megacephal* (Wilson, 1984) but not when only 50% of a caste was removed in *P. badius* (Kwapich and Tschinkel, 2013). In our study on *C. fellah*, despite most (i.e. 94.0%) foraging ants being removed in the forager removal treatment, no behavioral flexibility was observed. Our study brings therefore the first evidence of a true (i.e. not due to design) lack of behavioral flexibility in an ant species. Theoretically, behavioral flexibility should be especially present in unpredictable environments, where it could prove essential for colony survival. Conversely, more stable and predictable environment should not require a costly mechanism such as behavioral flexibility to evolve. In agreement with this theory, *C. fellah* gets food supply by tending honeydew-producing Hemiptera (Rosen, 1967) and *P. badius* gets food supply from the seeds stored in their nest (Kwapich and Tschinkel, 2013), providing both species with more stable and predictable food resources and less risky foraging than, for example, ant species solely depending on hunting. One could therefore make the hypothesis that the lack of behavioral flexibility in *C. fellah* and *P. badius* is due to their stable and predictable food resources. However, to further verify this theory, one would need to perform a removal experiments where most of *P. badius* foragers are removed and not only 50% like in the study of Kwapich and Tschinkel (2013). Also in agreement with this theory, *P. dentata* which has been shown to be flexible (Calabi and Traniello, 1989b) has also been shown to be a prominent predator (Whitcomb et al., 1982). However, in contradiction with this theory, the leaf-cutter ant *A. cephalotes*, which has been shown to be flexible (Wilson, 1983), has a stable and predictable food resource thanks to its fungi stores. For the other species that have been shown to be flexible, we lack information on the stability and predictability of their environment (*P. guilelmimueller*, *P. pubiventri* and *P. megacephal*). Overall, it seems therefore that no coherent environmental explanation to the differences of flexibility among the studied species can be found. To understand what species characteristics could predict its flexibility, similar removal experiments in more ant species should be performed.

We show that the social group structure (as measured by the proportion of ants without a social group and the number of social groups) after the removal is predicted by the null hypothesis, highlighting that the ants do not perform any active change of their social interactions to change the social group structure in response to the removal. Therefore, it seems that, in terms of social group structure, *C. fellah* stays passive in response to the removal.

Our results also highlight the key role played by the foragers for the colony-wide social network overall connectivity (measured here by the number of links and the strength of them). Six days or more after the forager removal, the number of interaction partners and the number of interactions per ants decreased, compared to the null hypothesis, significantly more than in the nurse and the control removal. The removal of the foragers therefore led to the highest disturbance of the network connectivity, highlighting the key contribution of the foragers to the network overall connectivity. This key role of the forager is in accordance with a study on the trophallactic fluid exchange network (Greenwald et al., 2015), which showed that foragers tend to have a higher number of large-volume trophallactic interactions (greater than 1% of the total net food flow over all trophallactic interactions) than other workers. In addition, foragers not only distribute food, they also receive food from non-foragers. Foragers are therefore not only the food source of the trophallactic network but also food receiver, for their own benefit or to transmit the food further to some other ants or brood. This double role highlights their importance in the trophallactic network and, as a trophallaxis event is a form of social interaction, in the more general social interaction network, in accordance with our results.

3.4 Individual contributions

RB wrote the chapter, under the supervision of DM and LK. RB and DM did the analysis, under the supervision of LK. DM and RB did the experiment, under the supervision of LK. AC provided technical support for the experiment.

3.5 Materials and methods

3.5.1 Experiment

To investigate whether and how an ant colony is resilient to the loss of some of its workers, we removed 25% of the workforce in 15 *Camponotus fellah* colonies. Nine colonies were six years old, three were three years old and three were two years old. Each colony had a queen, brood and about 200 workers. For the experiment, video-tracking took place in the same two-chamber system than the one used in Mersch et al. (2013b), Chapter 1 and Chapter 2 consisting of a constantly dark nest connected by a tunnel to a foraging arena exposed to 12 hours light - 12 hours dark cycles and in which ants could access food (sugar solution and protein solution) and water.

We chose to track ants seven days before the removal because our analysis (Chapter 1 and 2) of the data (Mersch et al., 2013b) of six unperturbed colonies of *C. fellah* showed that it was the minimum time range to properly assess the behavioral dynamics. We chose to track ants 13 days after the removal because that was the longest time span we could leave the colony without perturbing it to change the food reservoirs.

3.5.2 Analysis

All the models used in this chapter were linear mixed effect models and for all of them, we checked assumptions of normality, linearity, and homogeneity of variance of residuals.

3.5.2.1 Task specialization

The two main fixed effects (explanatory variables) of the linear mixed effect model are 'period' and 'treatment'. 'period' indicates whether we consider before or after the removal, and 'treatment' indicates which treatment is considered: nurse removal ('nr'), forager removal ('fr') or control removal ('cr'). The reference levels for the two main fixed effects are 'beforeRemoval' for 'period' and 'cr' (control removal) for 'treatment'. Interactions between those two main fixed effects were also considered. Our model has two interaction terms: one for the difference of the effect of removal between the forager removal and the control removal (interaction 1) and one for difference of the effect of removal between the nurse removal and the control removal (interaction 2). The p-value on the main effect of 'period' showed us whether, everything else being equal, there is a significant difference between the daily change of the average proportion of ants in the foraging box before removal and after removal in the control removal treatment. In addition and most importantly, the p-value of the two interaction terms showed whether, in the forager removal and in the nurse removal, this difference changed significantly (everything else being equal) compared to the control removal.

For this model and all other models used in this chapter, to account for the unexplained variation between colonies, ‘colony’ was included as a random effect. Finally, to avoid pseudo-replication stemming from the repeated measurement of the response (measured every day during multiple days), we added (as an additional random effect of all models) a random intercept and a random slope of the response with respect to time.

This model was created in ‘R’ (R Core Team, 2017) using the function ‘lmer’ of the ‘lme4’ package (Bates et al., 2015), and p-values were computed with the ‘lmerTest’ (Kuznetsova et al., 2017) package in ‘R’. See Appendix section 3.6.1.1 for the full ‘R’ formula for this model.

3.5.2.2 Social network analysis

3.5.2.2.1 Social network rewiring

For each network measure (degree, weight and strength), we calculated the change of the measure by subtracting the null hypothesis value from the observed values after the removal, and used this change as the response of a linear mixed effect model. The only fixed effect of the model was ‘treatment’.

The model was created in ‘R’ (R Core Team, 2017) using the function ‘lmer’ of the ‘lme4’ package (Bates et al., 2015). The p-values reported come from a pairwise post-hoc comparison and are corrected for multiple comparison with a single-step method from Simultaneous Tests for General Linear Hypotheses with the ‘multcomp’ (Hothorn et al., 2008) package in 'R'. See Appendix section 3.6.2.1 for the full 'R' formula for this model.

3.5.2.2.2 Social groups

To test whether the social groups reformed after the removal, we used the OLSOM (Lancichinetti et al., 2011) social group algorithm and measured every day the proportion of groupless ants (i.e. ants that cannot be attributed significantly to any social group by OSLOM) and the number of groups. We then applied the same test on the proportion of groupless ants and the number of groups than on the three network measures above.

It has to be noted that the groupless ants mainly appear in response to the removals (average proportion of groupless ants before removal = 4%, average proportion of groupless ants after removal = 17%). Therefore the proportion of groupless ants was a good first measure of the effect of removal on the social group structure. Adding the number of groups as a second measure of social group structure added more information about the effect of removal on the social group structure.

3.6 Appendix

3.6.1 Task specialization

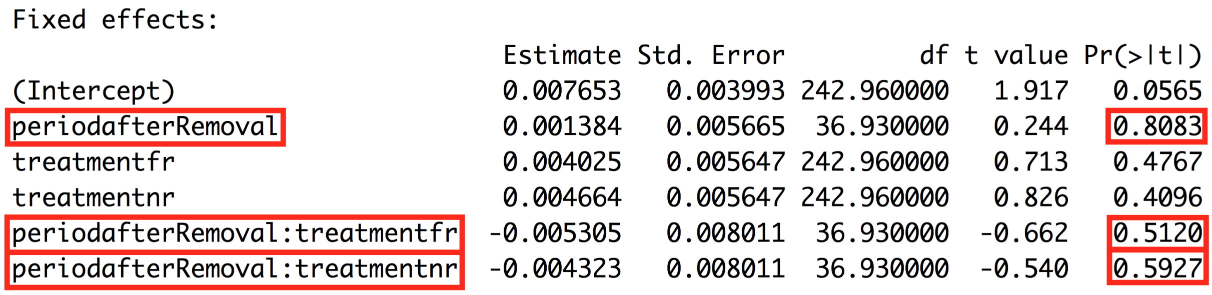
3.6.1.1 R formula of the linear mixed effects model

In 'R', the linear mixed effects model used to test the effects of the different treatments on task specialization is written:

```
lmer(
  daily_change_of_average_proportion_of_ants_in_foraging_box
                                ~ period*treatment + (day|colony)
                                                                    ).
```

3.6.1.2 Summary statistics table for the linear mixed effects model

TABLE 3.1: Summary statistics table for the fixed effects of the linear mixed effects model (see Materials and methods section 3.5.2.1 for more details).



```
Fixed effects:
                                 Estimate Std. Error         df t value Pr(>|t|)
(Intercept)                      0.007653   0.003993 242.960000   1.917   0.0565
periodafterRemoval               0.001384   0.005665  36.930000   0.244   0.8083
treatmentfr                      0.004025   0.005647 242.960000   0.713   0.4767
treatmentnr                      0.004664   0.005647 242.960000   0.826   0.4096
periodafterRemoval:treatmentfr  -0.005305   0.008011  36.930000  -0.662   0.5120
periodafterRemoval:treatmentnr  -0.004323   0.008011  36.930000  -0.540   0.5927
```

3.6.2 Social network analysis

3.6.2.1 R formula of the linear mixed effects model

In 'R', the linear mixed effects models used to test the effects of the different treatments on the rewiring of the social networks and on the social groups are all written:

```
lmer(
   (measure_on_network_after_removal -
         measure_on_network_under_null_hypothesis
                                   ~ treatment + (day|colony)
                                                           ).
```

3.6.2.2 Summary statistics tables for the post-hoc comparison tests on the linear mixed effects model

3.6.2.2.1 Social network rewiring

TABLE 3.2: **Table showing the detailed results of the post-hoc comparison tests for the effect of 'treatment' on the change of the mean number of interactions partners per ant** compared to null hypothesis, 1-5 days (**a**) and 6-12 days (**b**) after the removal. The "Lin. Hyp." column indicates the two treatments we are comparing. 'cr'=control removal, 'nr'=nurse removal and 'fr'=forager removal. Significance codes : $***= [P < 0.001]$, $** = [P < 0.01]$, $* = [P < 0.05]$. See Appendix section 3.6.2.1 for the 'R' formula and see Materials and methods section 3.5.2.2 for more details.

a 1-5 days after removal:

Lin. Hyp.	Estimate	SE	z	P(>|z|)
cr - nr == 0	−2.22	2.65	−0.838	0.6794
fr - nr == 0	−6.20	2.65	−2.339	0.0506
fr - cr == 0	−3.98	2.65	−1.501	0.2904

b 6-12 days after removal:

Lin. Hyp.	Estimate	SE	z	P(>|z|)	
cr - nr == 0	−1.66	2.28	−0.728	0.7470	
fr - nr == 0	−12.76	2.28	−5.599	0.0000	***
fr - cr == 0	−11.10	2.28	−4.871	0.0000	***

TABLE 3.3: **Table showing the detailed results of the post-hoc comparison tests for the effect of 'treatment' on the change of the mean number of interactions per interacting ant pair** compared to null hypothesis, 1-5 days (**a**) and 6-12 days (**b**) after the removal. The "Lin. Hyp." column indicates the two treatments we are comparing. 'cr'=control removal, 'nr'=nurse removal and 'fr'=forager removal. Significance codes : $*** = [P < 0.001]$, $** = [P < 0.01]$, $* = [P < 0.05]$. See Appendix section 3.6.2.1 for the 'R' formula and see Materials and methods section 3.5.2.2 for more details.

a 1-5 days after removal:

Lin. Hyp.	Estimate	SE	z	P(>|z|)
cr - nr == 0	−0.44	0.48	−0.917	0.6298
fr - nr == 0	−0.96	0.48	−1.985	0.1158
fr - cr == 0	−0.52	0.48	−1.069	0.5335

b 6-12 days after removal:

Lin. Hyp.	Estimate	SE	z	P(>|z|)	
cr - nr == 0	−0.44	0.39	−1.119	0.5021	
fr - nr == 0	−1.87	0.39	−4.755	0.0000	***
fr - cr == 0	−1.43	0.39	−3.635	0.0009	***

TABLE 3.4: **Table showing the detailed results of the post-hoc comparison tests for the effect of 'treatment' on the change of the mean number of interactions per ant** compared to null hypothesis, 1-5 days (**a**) and 6-12 days (**b**) after the removal. The "Lin. Hyp." column indicates the two treatments we are comparing. 'cr'=control removal, 'nr'=nurse removal and 'fr'=forager removal. Significance codes : $*** = [P < 0.001]$, $** = [P < 0.01]$, $* = [P < 0.05]$. See Appendix section 3.6.2.1 for the 'R' formula and see Materials and methods section 3.5.2.2 for more details.

a 1-5 days after removal:

Lin. Hyp.	Estimate	SE	z	P(>|z|)
cr - nr == 0	−52.01	56.67	−0.918	0.6291
fr - nr == 0	−128.27	56.67	−2.264	0.0610
fr - cr == 0	−76.27	56.67	−1.346	0.3698

b 6-12 days after removal:

Lin. Hyp.	Estimate	SE	z	P(>|z|)	
cr - nr == 0	2.79	43.32	0.064	0.9977	
fr - nr == 0	−176.36	43.32	−4.071	0.0001	***
fr - cr == 0	−179.15	43.32	−4.135	0.0001	***

3.6.2.2.2 Social groups

TABLE 3.5: **Table showing the detailed results of the post-hoc comparison tests for the effect of 'treatment' on the change of the proportion of ants without social group** compared to null hypothesis, 1-5 days (**a**) and 6-12 days (**b**) after the removal. The "Lin. Hyp." column indicates the treatment (or difference of treatments) we are comparing to 0. 'cr'=control removal, 'nr'=nurse removal and 'fr'=forager removal. Significance codes : $*** = [P < 0.001]$, $** = [P < 0.01]$, $* = [P < 0.05]$. See Appendix section 3.6.2.1 for the 'R' formula and see Materials and methods section 3.5.2.2 for more details.

a 1-5 days after removal:

Lin. Hyp.	Estimate	SE	z	P(>|z|)
nr == 0	0.04	0.07	0.542	0.9432
cr == 0	0.11	0.07	1.591	0.3609
fr == 0	−0.07	0.07	−0.995	0.7334
cr - nr == 0	0.07	0.10	0.741	0.8690
fr - nr == 0	−0.11	0.10	−1.087	0.6763
fr - cr == 0	−0.18	0.10	−1.828	0.2416

b 6-12 days after removal:

Lin. Hyp.	Estimate	SE	z	P(>|z|)
nr == 0	−0.05	0.07	−0.685	0.8933
cr == 0	0.09	0.07	1.192	0.6088
fr == 0	−0.14	0.07	−1.869	0.2238
cr - nr == 0	0.14	0.10	1.327	0.5210
fr - nr == 0	−0.09	0.10	−0.837	0.8224
fr - cr == 0	−0.22	0.10	−2.164	0.1223

TABLE 3.6: **Table showing the detailed results of the post-hoc comparison tests for the effect of 'treatment' on the change of the number of social groups** compared to null hypothesis, 1-5 days (**a**) and 6-12 days (**b**) after the removal. The "Lin. Hyp." column indicates the treatment (or difference of treatments) we are comparing to 0. 'cr'=control removal, 'nr'=nurse removal and 'fr'=forager removal. Significance codes : $* * * = [P < 0.001]$, $** = [P < 0.01]$, $* = [P < 0.05]$. See Appendix section 3.6.2.1 for the 'R' formula and see Materials and methods section 3.5.2.2 for more details.

a 1-5 days after removal:

Lin. Hyp.	Estimate	SE	z	P(>|z|)
nr == 0	−0.09	0.22	−0.414	0.9734
cr == 0	−0.05	0.22	−0.249	0.9939
fr == 0	0.29	0.22	1.309	0.5330
cr - nr == 0	0.04	0.31	0.117	0.9994
fr - nr == 0	0.38	0.31	1.218	0.5917
fr - cr == 0	0.34	0.31	1.101	0.6669

b 6-12 days after removal:

Lin. Hyp.	Estimate	SE	z	P(>|z|)
nr == 0	0.06	0.21	0.267	0.9926
cr == 0	−0.20	0.21	−0.933	0.7696
fr == 0	0.12	0.21	0.561	0.9378
cr - nr == 0	−0.26	0.30	−0.848	0.8165
fr - nr == 0	0.06	0.30	0.208	0.9965
fr - cr == 0	0.32	0.30	1.056	0.6955

3.6.3 Social dynamics before removal

For information, we draw the dynamics of social maturity (i.e. the *social dynamics*) before the removal (Fig. 3.7; for more details on this methodology see Chapter 1). Because of the high number of groupless ant after the removal, it was not possible to run FacetNet (Lin et al., 2009) after the removal and it was therefore not possible to obtain the dynamics of social maturity after removal. To study the effect of removal on temporal polyethism, we therefore focused on task dynamics using the foraging transition rate (defined in Results section 3.2.2.1). This analysis of the effect of removal on the foraging transition rate is presented in this chapter in Results section 3.2.2.1 and the methodology is presented in Materials and methods section 3.5.2.1.

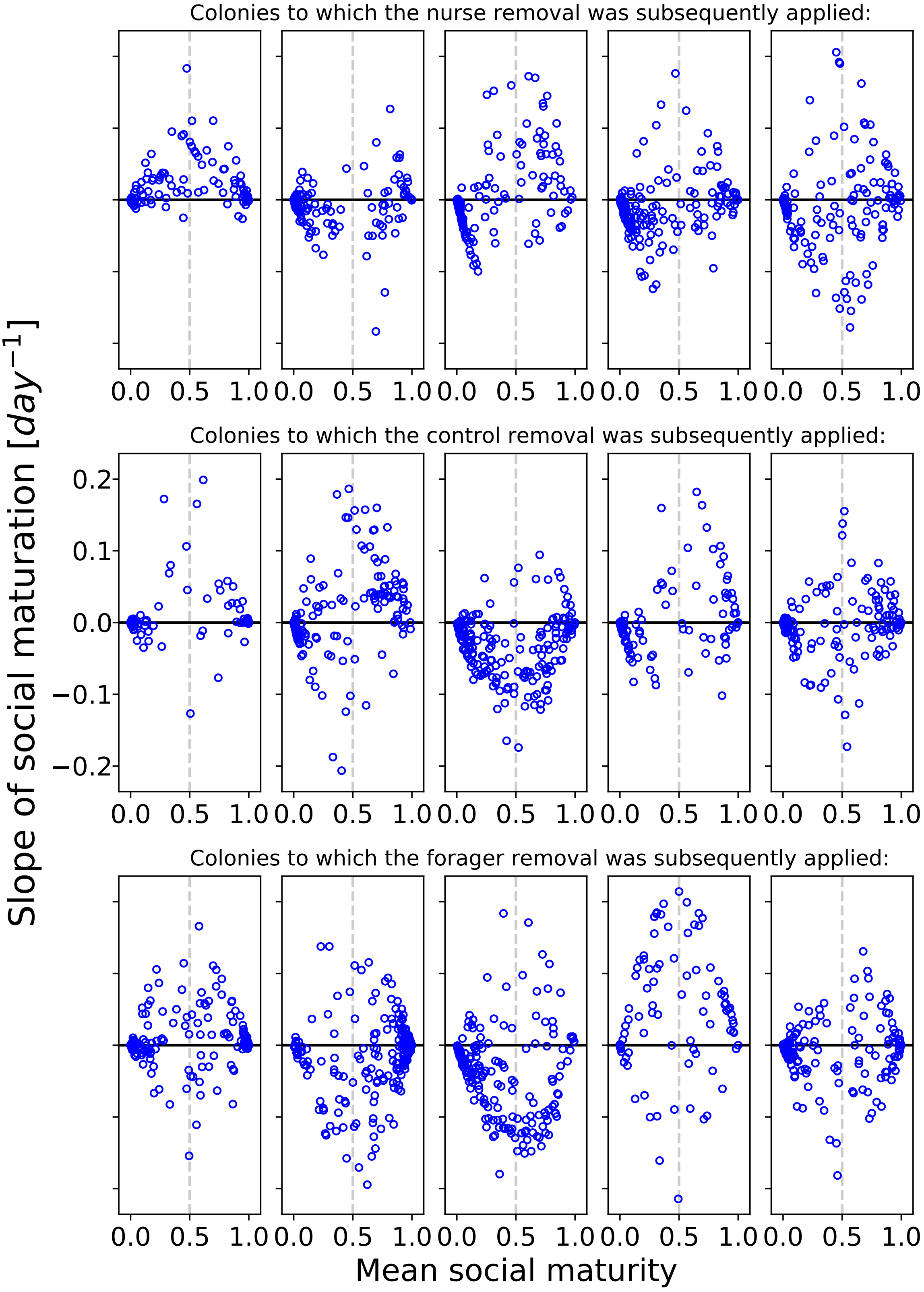


FIGURE 3.7: **Workers' social dynamics before removal in the 15 colonies.** Slope of linear regression of social maturity upon the seven days before removal as a function of the seven-day mean social maturity. Each panel represents a different colony, each point a different ant. For more details see Chapter 1.

Perspectives

In Chapter 1 and 2, we quantitatively described individual ant behavior with two important aspects of individual behavior both related to division of labor: social maturity and task specialization. However, two workers could have the same value of social maturity and task specialization but differ in their level of activity. Activity levels can be highly variable in ant colonies and a significant fraction of the worker are not active at all (in the lab: Charbonneau and Dornhaus, 2015; in the field: Charbonneau et al., 2015). However, how activity levels influence division of labor and social interactions is poorly understood. Future work could measure the activity levels of all workers and compare it to their task and social dynamics as well as to their SSZ.

In Chapter 2, our results highlight links between individual-level dynamic properties (task and social dynamics) and colony-level structures (the nest-entrance distance and the spatial segregation of the ants). However, these results were purely correlational. For example, the positive correlation between social dynamics and the distance between the brood pile and the nest entrance raises the question whether there is a causal link between the brood-entrance distance and the social dynamics. To answer these questions, one would need to manipulate experimentally the location of the brood pile. To do so without disturbing the colony, one could cool the nest slightly and create a warmer spot whose position one can control. The warm spot would provide the preferred temperature for the brood and thus attract the ants to put the brood pile there. One would then compare four treatments and two controls. One would induce the ants to move the brood pile slowly from the further corner of the nest towards the nest entrance in a first treatment and from the nest entrance away to the furthest corner of the nest in a second treatment. One would also induce the brood pile to remain in the corner furthest from the nest entrance in a third treatment and as close as possible to the nest entrance in a fourth treatment. To distinguish what is due to the movement of the brood pile and what is due to the change of temperature of the nest, one would do control treatments where one keep the ants and the brood in a homogeneous temperature nest and one lets them choose the position of the brood pile. In the first control, one would put a heat source just below the brood pile once its location is chosen by the ants and slightly cool down the rest of the nest. In the second control treatment, one would maintain the homogeneous temperature conditions in the nest. We predict that in the two treatments in which one induces the ants to move the brood pile, the social dynamics will change accordingly, with ants changing less and less and slower and slower from the nurse to the forager social group, potentially leading to a reversal of the social dynamics (i.e. from forager to nurse instead of from nurse to forager). If this change occurs, one would conclude that a causal link exists and is it the position of the brood pile that causes the change of social dynamics. If no reversal occurs, one would conclude that either it is the change of social dynamics that causes the brood pile to move or that no causation underlies the observed correlation but that some other factor (e.g. a colony effect) triggers both the social dynamics change and the brood pile movement.

Finally, in Chapter 3, we show that *C. fellah* do not flexibly compensate for the loss of specific workforce (nurses or foragers), perhaps because specific workforce loss does not happen often enough in the field to counterbalance the cost of such a flexible behavioral mechanism. However, ant colonies are oftenexposed to direct changes in workload in a particular task (e.g. increase in the number of brood laid by the queen in preparation for the mating flight [Hölldobler and Wilson, 1990] or decrease in food resources due to a drought). Such changes in workload in a particular task have been shown, in the ant *Temnothorax albipennis*, to trigger behavioral flexibility by reallocation of the workforce (Robinson et al., 2009a). In future work, one could, for example, manipulate the workload of nurses by varying the number of larvae per colony. Workers readily accept larvae from foreign colonies and raise them as their own (Danielle Mersch, personal communication). In a first treatment, one would add larvae to increase the workload of nurses. In a second treatment, one would zero the workload of nurses by removing all larvae leaving only pupae and eggs that require little attention and no feeding from the workers. Finally, in a control treatment one would exchange larvae between colonies without changing the count of larvae in either colony, thereby reproducing the same disturbance without changing the workload. One would track all colonies for another 14 days to assess whether colonies reallocate workers to compensate for the change in the workload. If colonies are able to allocate workers flexibly depending on workload, we predict an acceleration of the foraging transitionrate in the brood reduction treatment compared to the control, and deceleration of the foraging transitionrate in the brood increase treatment.

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