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MEMÓRIA E SOCIALIDADE

**COMO O RECONHECIMENTO INDIVIDUAL
AFETA FORMAÇÃO DE GRUPOS**

São Paulo
2016

**MEMÓRIA E SOCIALIDADE
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AFETA FORMAÇÃO DE GRUPOS**

**MEMORY AND SOCIALITY
HOW INDIVIDUAL RECOGNITION AFFECTS
GROUP FORMATION**

Versão original da tese apresentada ao
Instituto de Biociências da Universidade de
São Paulo para obtenção do título de Doutor
em Ciências, na área de Ecologia

Orientador: Roberto André Kraenkel

São Paulo
2016

Ficha catalográfica

Rios, Vitor Passos

Memória e Socialidade

Número de páginas: 71 páginas

Tese (Doutorado) - Instituto de Biociências da Universidade de São Paulo. Departamento de Ecologia.

1. Socialidade 2. Memória 3. Modelagem computacional. 1. Sociality 2. Memory 3. Computer modelling. I. Universidade de São Paulo. Instituto de Biociências. Departamento de Ecologia.

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Agradecimentos

Gostaria de agradecer às pessoas que tornaram este doutorado possível e agradável.

A CAPES e à Fapesp pelo apoio financeiro (Processo 2012/13779-3), essenciais para a realização deste projeto.

A Roberto, por ter me orientado e acompanhado nesses quatro anos. Quando eu mandei o primeiro email com uma vaga ideia de projeto eu não tinha ideia de o quanto tudo ia mudar e o quanto eu ia aprender. O tempo que passei no Grupo de Biologia Matemática, com nossas discussões e reuniões, me fez crescer imensamente como cientista.

A Paulo Inácio, pelo apoio que sempre me deu, na seleção e nos momentos difíceis ao longo do caminho.

A Paulo Inácio, Miúdo e Glauco, por terem criado na Lage um ambiente extremamente acolhedor e estimulante. O espírito de coleguismo e colaboração de vocês é um exemplo de como deve ser qualquer ambiente, dentro e fora da academia.

Aos colegas e amigos da Lage e agregados, Solimary, Ayana, Danilo, Erika, Sara, D2, Mandai, Lucas, Taio, Paulinha, Pietro, Lygia, Billy, e vários outros que passaram pela Lage nesses quatro anos, pelas risadas, cafés, discussões e conversas, no Puxadinho e fora dele.

A Melina, Pamela, Sheina, Catalina, William, Sara e Ayana, por terem aceito a loucura de fazer um curso megalomaniaco feito a EcoEscola, e ter feito dele um sucesso tão grande, que conseguimos convencer pessoas a fazerem de novo, e tá a caminho de ter uma terceira.

A Garcia, que é sempre fonte de inspiração, por ter moldado meu caminho como modeleiro desde a graduação, por ter me incentivado a seguir com a academia, e por me lembrar que mesmo quando o projeto dá errado, o importante é estar feliz com seu trabalho.

Agradeço também a Charbel e Peu, que primeiro me mostraram os caminhos da ciência no LVT, em 2003. Ainda levo comigo as lições que aprendi nos anos que passei com vocês na Ufba. Este trabalho é descendente direto dos trabalhos com os *yonenagae*, com os quais comecei meus estudos sobre comportamento social, e muito do que está aqui é devido ao que aprendi no LVT.

A meus tios, Cristiana e Marcus, que me receberam em São Paulo e me apoiaram neste caminho.

A meu afilhado e sobrinho Bernardo, que divide comigo o amor pela natureza, o gosto pelos pokemons e super-heróis, e que me faz querer continuar sendo biólogo só pra ver o orgulho no rosto dele.

A meus pais, porque foram eles que me ensinaram o prazer do conhecimento e me incentivaram a seguir a pesquisa. Amo vocês.

E finalmente agradeço a Vanessa, a quem dedico esta tese, por ter me encorajado e se jogado comigo nesta aventura de sair de Salvador, mesmo sem saber no que ia dar, por ter encarado frios glaciais e calores infernais em São Paulo, por comer coisas estranhas comigo, pelas nossas viagens juntos, por dividirmos nossas vidas, por me dar forças e me aguentar. Te amo muito.

Resumo

Nesta tese, nós investigamos os efeitos do reconhecimento individual sobre a formação de grupos. No capítulo 2 nós revisamos o conhecimento sobre as bases evolutivas do comportamento social, e no capítulo 3 nós nos focamos num mecanismo específico, o reconhecimento individual. Nós revisamos as bases do reconhecimento individual para construir um modelo mínimo de como o reconhecimento individual funciona, visando investigar suas consequências para a estrutura social dos animais. O capítulo 4 é construído como uma introdução à modelagem computacional. Utilizando a técnica de modelagem baseada em agentes, no capítulo 5 nós criamos uma população de indivíduos que são capazes de reconhecer uns aos outros e de lembrar as interações passadas. Nós demonstramos que a presença de memória e reconhecimento individual é capaz de afetar dramaticamente o número e tamanho dos grupos formados. Quando não há memória, os indivíduos formam muitos grupos pequenos, sem estrutura definida. Na presença de memória, os indivíduos se agrupam em clusters cerca de uma ordem de grandeza maiores, e consequentemente menos grupos são formados. Nós demonstramos também que a organização interna dos grupos muda: na presença de memória, os grupos apresentam modularidade maior, isto é, há formação de subgrupos dentro do cluster, onde há uma maior frequência de interações entre os indivíduos. Nossos resultados também mostram a influência da densidade para a formação de grupos: quando a densidade é baixa demais, mesmo na presença de reconhecimento individual, as probabilidades de encontro são baixas demais para que os efeitos do reconhecimento sejam percebidos, e o inverso ocorre com densidades altas demais.

Abstract

In this thesis, we investigate the effects of individual recognition on group formation. In chapter 2 we review the current knowledge on the evolutionary basis of social behavior, and in chapter 3 we focus on a specific mechanism, individual recognition. We review the basis of individual recognition to devise a minimal model of how individual recognition works, aiming to investigate its consequences on the social structure of animals. Chapter 4 is structured as an introduction to computational modelling. Using agent-based modelling, in chapter 5 we build a population of individuals which can recognize one another and can remember past interactions. We show that presence of memory and individual recognition can dramatically affect the number and size of groups. in the absence of memory, individuals form small, unstructured groups. in the presence of memory, individuals form clusters about an order of magnitude greater in size, and consequently less groups are formed. we also show that the group's internal structure changes: with memory, group modularity is higher, that is, subgroups are formed within the cluster, in which frequency of interactions is greater than outside the subgroup. Our results also show that density affects group formation: when density is low, even with individual recognition, encounter probabilities are so low that recognition's effects are not visible, and the opposite holds for too high densities.

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1 — Presentation

1.1 Thesis structure

In this thesis, we discuss animal sociality, and specifically the importance of social recognition on group formation. Our work is guided by an old question in behavioral ecology: What mechanisms cause animals to group? We also intend this thesis, especially Chapter 2 - Sociality and Chapter 4 - Model building, to serve as an introductory text on behavioral ecology and agent-based modelling, so in the text we strive to reach a middle ground on technical terms in both behavioral ecology and modelling. To do this, we will approach subjects from chapters 3 and 5 in more depth on the other chapters. Some slight repetition is unavoidable, but we will keep it to a minimum. Throughout the text, important concepts will appear in boxes, and quick definitions of terms will appear on footnotes.

Below we summarize each chapter's contents:

- **Chapter 2 - Sociality.** In this chapter we review models of sociality and present the question which guided our entire work: How does recognition affect animal sociality? We also look at some important definition of behavioral terms which are used throughout this thesis. More precisely, we define recognition in terms of memory and social behaviors in terms of movement, to lay the foundations for our model
- **Chapter 3 - Recognition And Sociality.** Here we present a general review of the factors involved in Individual Recognition, and the effects it can have on animal sociality. We briefly summarize the neurological substrate of recognition, and present modelling as a

powerful tool to generate and test hypothesis in behavioral ecology.

- **Chapter 4 - Model building.** To approach our question of whether groups caused by memory-based interactions are different from externally caused ones, we created a model of interacting individuals on whom we can turn recognition on and off. Here we will present in detail how our model of individual recognition works and present some results which have guided our decisions throughout this work.
- **Chapter 5 - Do I know you?** In this chapter we present in a concise manner the main results of our work. We show how groups created from memory-influenced interaction are quantifiably different from groups created from random-based interactions. Here we present the ODD protocol of the model, which aims to describe our model in a reproducible and reimplementable manner. We also present the algorithms used in our analyses, as they are novel in behavioral ecology research and we believe them to be of use in other areas. This chapter has been submitted for publication in *PLOS ONE*, and has had its figures, formatting and bibliography styles slightly adapted to fit the overall thesis format, but the contents and data were not altered.

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2 — Sociality

2.1 Sociality, its causes and consequences for animals

Social living varies greatly, from solitary individuals who almost never meet a conspecific¹ to individuals who live their entire lives inside a burrow with sometimes thousands of siblings. Given that group living is neither rare nor the absolute norm, and that group sizes can vary widely even within the same species of animals, an obvious question is: what are the causes and consequences of grouping behavior? We will look at them below, and will focus ourselves on a particular cause of grouping in the next chapters. Our goal here is not to give an exhaustive review of each topic, but a general overview of their basic concepts and their contributions to the understanding of the evolution of sociality.

2.1.1 Kinship and reproduction

Insect societies have long been a puzzle. Why would something like a beehive evolve? Why would animals give up reproduction in favor of others? Even considering that bee workers are infertile and thus cannot relinquish what they do not have, the same pattern is seen in other societies without physiologically-determined castes², in which all members are fertile and could reproduce, as is in many vertebrate societies, and yet they do not. Vehrencamp (1979) has termed this partitioning of reproduction *Reproductive Skew*.

¹**Conspecific:** a member of the same species

²**Caste:** An extreme form of labor division in a social species. Examples would be the workers, soldiers and queens of ant colonies, which are physically quite different and have completely separate roles in the nest

Box 2.1 — On kin selection and fitness.

Before we proceed to talk about the evolution of sociality, we must first make a detour to talk about how sociality can be selected. In other words, we will talk about *fitness*. Fitness is an abstract concept, but for our purposes, fitness can be understood as a measure of the overall reproductive success of an individual. Hamilton (1964a; 1964b), talking about the evolution of sociality, stated that a trait would be positively selected whenever the benefits associated with having it outweighed its costs. More formally, a trait is selected whenever its cost in fitness (C) is smaller than its benefits in fitness (B).

Hamilton proposes an extension to the concept of fitness, that of fitness gained from the reproductive success of kin, *inclusive fitness*. Inclusive fitness helps explain the paradox of altruism: why would animals favor others in detriment of themselves? Animals have been seen to help raise the offspring of kin, to share food, and to emit alarm calls that attract the attention of predators to themselves when other are at risk. All these actions should be selected against if only direct fitness is taken into account, as their cost is greater than their benefits. By raising other's offspring, one expends energy that could be used to raise one's own. Likewise, food shared is food not eaten, and to call attention to oneself can be equal to suicide. However, taking inclusive fitness into account, these actions can be seen as improving the fitness of relatives. Given that a relative has a high probability to share part of your genes (the closer the relation the higher the portion shared), then an act that increases the fitness of a relative also increases one's own fitness by a small margin. Letting r be the coefficient of relatedness, that is, the proportion of one's genes a relative is likely to share, an altruistic act would be selected if:

$$C < rB \quad (2.1)$$

Altruism is selected if the fitness benefit to the receiver, adjusted by the relatedness to the giver, is greater than the cost to the giver, or in other words, if the overall fitness of the giver is increased by more than the direct cost in fitness the giver pays for the act. Inequality 2.1 is known as Hamilton's rule, and is the basis for most explanations of sociality that deal with kinship and fitness, a theory known as *kin selection*. This theory is extremely important to explain societies where a portion of individuals relinquish their reproduction in favor of a small portion of the group and relatedness coefficients are extremely high, as is seen in honeybees or ants, and indeed is the foundation for much of the theory of evolution of sociality that we will review in this chapter, and practically all evolutionary explanations of sociality (specially eusociality) can be traced back to it. Kin selection has recently come under attack as being unrealistic by Nowak, Tarnita, and Wilson (2010), but the debate is far from settled, and it has strong defenders, having been tested time and again (Abbot et al. 2011; Birch and Okasha 2015).

Reproductive skew

Reproductive skew can be thought of in terms of the proportion of total reproduction for which each member of the group is responsible. In an *egalitarian* society, all members get an approximately equal share, and distribution of reproduction is uniform (Fig 2.1). In a society which exhibits reproductive skew, a few members are responsible for the majority, perhaps the entirety, of reproduction. Suppose that the group's realized reproduction is k^3 , and solitary fitness is x_d for the individual which dominates reproduction (sometimes called the *allocator*) and x_s for the subordinates. If the subordinate is responsible for a percentage p of the total reproduction, and r is the relatedness coefficient, then skew can be positively selected whenever p is between a minimal p_{min} , and a maximum p_{max} (Nonacs and R. Hager 2011):

$$p_{min} = \frac{x_s - r \cdot (k - x_d)}{k \cdot (1 - r)} \quad (2.2)$$

$$p_{max} = \frac{k - x_d - r \cdot x_s}{k \cdot (1 - r)} \quad (2.3)$$

p_{min} is the minimal percentage of reproduction from which it is advantageous for the subordinate to remain in the group, and p_{max} represents the maximum reproduction the dominant can afford to relinquish to the subordinate without incurring in reproductive loss for itself.

Figure 2.1: **Reproductive skew.**A: distribution of reproduction in an egalitarian society is approximately uniform B: a heavily skewed society, where only a few individuals are responsible for the bulk of reproduction. In this case probability of reproduction decays exponentially. Individuals are sorted by number of offspring. In both cases, average number of offspring is 14 per individual

³**A note on notation:** Reproductive fitness literature is fraught with notation problems, with the same variables receiving different symbols depending on the author. In this section we will follow Nonacs and R. Hager (2011) for a matter of coherence, even when the original texts use other notations. Indeed, we must note that those authors dedicate a significant section of their paper to dealing with this problem.

Interestingly, reproductive skew theory shows that it is not necessary for the individuals in the group to be closely related, as long as collective reproductive success k is high enough, above a minimal threshold:

$$k_{min} = x_d + x_s, \quad (2.4)$$

that is, if both parties reproduce more from being in the group than outside of it.

This basic model, called the *transactional model* has been extended and altered many times. One interesting extension is adding the value of a territory to the equation. If we call c the probability of the subordinate winning a territory dispute, S the fitness gained from being in the territory and L the fitness individual fitness after leaving,

$$x_d = (1 - c) \cdot S + c \cdot L \quad (2.5)$$

$$x_s = c \cdot S + (1 - c) \cdot L \quad (2.6)$$

by substituting in Equation 2.4 we get that staying in the group is advantageous whenever the territory is a significant boost over solitary reproduction:

$$k_{min} = \overbrace{(1 - c)S + cL}^{x_d} + \overbrace{cS + (1 - c)L}^{x_s} \quad (2.7)$$

Note that the model allows for incomplete skew, that is, reproduction of both the dominant and the subordinate, as is seen, for instance in some mammal societies like primates. Complete skew, where the subordinate does not breed can be achieved whenever the relatedness coefficient r is greater than zero and $k > x_d + x_s/r$. This is more common in the so-called *eusocial*⁴ insects, but can be also seen in some vertebrate societies, like the eusocial naked mole-rat *Heterocephalus glaber* (Jarvis and Sherman 2002) and others (Clutton-Brock 2002).

Extensions of the reproductive skew models introduce the notion of *incentives*, extra reproduction the dominant concedes to the subordinate in order to dissuade it from fighting for dominance and taking over the territory. Another extension are the *compromise* models, which assume that there is competition inside the group for reproduction. A key feature of compromise models is that both dominant and subordinate invest resources in the contest, in amounts termed x and y respectively, and the subordinate is assumed to have a lower competitive ability, represented by b . Total reproductive output is decreased by $1 - x - y$, due to resources being allocated to fighting and not to reproducing (Johnstone 2000).

⁴**Eusocial:** usually describes a society with only one reproductive female and a sterile caste. The concept of eusociality and the evolutionary paths leading to it are interesting and hotly debated, but would be a thesis unto itself.

Reproductive skew models, because they are based on fitness allocation, are troublesome to parameterize⁵, specially compromise models, where x , y and b are not easy (or sometimes even possible) to measure. Even so, they provide a strong framework for the evolution of societies with different levels of skew, and there have been quite a few studies which have tested and corroborated its predictions across many different vertebrate and invertebrate taxa. We point the reader to (Nonacs and R. Hager 2011) for an in-depth review and synthesis of reproductive skew models and its tests.

2.1.2 Resources

Animals live and die by their resources: microhabitats, food, water, shelter, are all determinants of animal distribution. The Resource Distribution Hypothesis (RDH), formulated by Macdonald (1983), originally only for carnivores, later expanded to other taxa, states that "(...) *there are ecological circumstances in which the benefits of 'spatial groups'*⁶ (and equally perhaps the evolutionary origins of contemporary highly social groups) may have little or nothing to do with advantages directly consequent on sociality. Rather, resource (particularly food) dispersion is fundamental to the spacing and structure of carnivore society in that it may set the limits to the group and territory sizes within which other combinations of selective pressures operate". In other words, there are cases in which resource distribution is a more powerful driver of animal aggregation than social, reproductive or predatory pressures. We use food as an example resource here, but there is no reason why RDH would not work with other resources, *e.g.* refuges or nesting sites.

These effects are often seen when resources are unevenly distributed, either in time or in space, so that an individual or pair of individuals (called "primaries") would have to hold a territory large enough that there is at least one patch able to sustain them at any time. Carr and Macdonald (1986) liken this to a game of dice: if having enough food for the night is an all-or-nothing event, like rolling a six on a game of dice, it makes sense to have a large number of dice (food patches) to throw each night, to guarantee that, with reasonable odds, at least one six will be rolled on any given night. The higher the number of dice, the higher the probability of rolling more than one six. Thus, just by statistically guaranteeing food for at least one night inside its patchy territory, the primary actually holds a number of available, unused food patches,

⁵**Parameterize:** to obtain values for the parameters of the model equations from actual data

⁶emphasis ours

as can be seen in Fig. 2.2. The immediate consequence of this is that the average richness of the whole territory is higher (perhaps much higher) than what is needed to support the primaries. These supernumerary food patches can be exploited by other individuals (the secondaries) at little to no cost to the primaries. Indeed, defending these patches from the secondaries can mean an increase in energy demand by the primaries. Thus, even in the absence of benefits to the primary, and even in the absence of interaction (other than proximity) between primaries and secondaries, increased group sizes can happen, a situation Macdonald (1983) calls "a spatial group", a concept to which we will return many times in this thesis.

The benefit to the secondary is evident: it has access to food it wouldn't have otherwise. Even if the primary always takes the best, most productive patches, statistically the chance of finding some food in the surplus patches is better than a random walk, due to the very patchiness. The primaries do not need to benefit directly from the secondary to allow its presence, as long as they do not suffer loss in fitness. The addition of a secondary can be beneficial to the primary if, for instance, it helps in defending the territory. If the secondary is related to the primary, such

Figure 2.2: The Resource dispersion Hypothesis. Assuming that a territory has 14 patches, and resources are normally distributed with a given standard deviation, we plot the distribution of resources. Assuming that each animal needs 1 Resource Unit (RU), a pair of primaries would need 2 RU to survive, and each added secondary would require an extra 1 RU. In A, the hatched area represents the probability that the territory produces at least 2 RU (95% in this case), and the green area represents the probability of producing enough food for primaries plus one secondary (90%) In B, we have two territories. Red is a low-heterogeneity territory (standard deviation of richness is 1), and blue is a high-heterogeneity one ($sd = 3$). The area under each curve is one. The black vertical line represents the necessary RU for a pair of primaries, and the green vertical line represents the RUs needed to support a pair of primaries plus one secondary. The integral of the area to the right of the green line represents the probability of the territory producing at least enough food for three occupants, 90% in the blue curve and 72% in the red one, respectively. This shows that a more variable environment can support larger group sizes, as the probability of having surplus food is higher. Image adapted from Macdonald and Johnson (2015) with permission.

as an offspring which delayed dispersing, then the primary also accrues benefits from indirect fitness, and this grouping would be positively selected. It must be emphasized that RDH presents only a scenario in which group formation *can* happen, not that it is a determinant of group formation in all, or even most, cases of social species. If the presence of one or more secondaries is too costly for the primaries, then we can expect that there will be no incentive in terms of fitness for the primary to allow their presence.

RDH does not discuss what makes an animal a primary or secondary, or any consequences of this hierarchy other than access to the patches. It has often been criticized as an *a posteriori* explanation without testable predictions, however, it does provide rigorous predictions, and has been subjected to many field tests (Macdonald and Johnson 2015). The predictions of RDH are:

- Group size is not directly correlated to territory size
- Territory size is determined by resource dispersion
- Group size is determined by resource heterogeneity
- Group size is determined also by total richness of resources

These clear prediction make RDH suitable for field tests, and indeed, there have been several that found support for its predictions, mostly with land mammals and a few birds (*e.g.* Cortés-Avizanda et al. (2011); Herrera and Macdonald (1989); Johnson, Jetz, and Macdonald (2002); Johnson, Kays, et al. (2002); Silva, Woodroffe, and Macdonald (1993); Spong (2002); Vangen et al. (2001)), but a few with invertebrates as well (*e.g.* Tanner and Jackson (2012)). We refer the reader to Macdonald and Johnson (2015) for an in-depth review of RDH, specially its criticisms and field tests.

2.1.3 Selfishness

Selfish herd is a term introduced by Hamilton (1971) himself, as an "*antithesis to the view that gregarious behaviour is evolved through benefits to the population or species*", in his own words. In this work, he proposes a model of selfish animals, each seeking only to minimize it's own risk of predation, which quickly goes from a random distribution to one where all individuals are tightly packed together. The selfish herd instinct is based on reducing the "domain of danger", that is, the empty, vulnerable space between the animal and a conspecific. Though there is some disagreement about the movement rules of animals in these herds (James, Bennett, and Krause 2004), it is remarkable that packing arises without communication, planning and even without

Figure 2.3: **The selfish herd.** Results from a simulation recreating Hamilton's model. A) initial, random, distribution of individuals, B) Clustered distribution of individuals after a few rounds of seeking the closest neighbor. Colored areas represents the domain of danger of each individual. Simulation run on Netlogo, code available on GitHub (https://github.com/vrios/Selfish_herd).

individuals knowing where the predator is going to strike. In Fig 2.3, we show a simulation of the selfish herd effect based on a simple rule: move towards your closest neighbor. In this simulation, no communication takes place, and yet the animals form aggregates.

There is experimental evidence that animals do exhibit this group-seeking behavior when there is risk: fish tend choose to join larger shoals even in the absence of predators, and threat of predation intensifies this effect (Ashley, Kats, and Wolfe 1993; M. C. Hager and Helfman 1991; Krause and Godin 1994). It has been shown that animals in herds can receive a decrease in predation risk greater than what would be expected, with the risk sometimes falling to less than half of what it was when solitary (Neill and Cullen 1974). Sorato et al. (2012) also found that birds in larger groups, though more likely to encounter predators, were less likely to be attacked by them. Evidence for this is also available in other animal groups: In a review, Hill and Lee (1998) have found that group size was strongly linked to predation risk in 39 species of Cercopithecoid monkeys. The protection inside the herd has been ascribed to not only an statistical decrease in the probability of any one individual being attacked, but also to a confusion effect, in which the number and movement of grouped prey make it difficult for the predator to successfully attack, futher increasing individual protection (Schradin 2000; Smith and Warburton 1992).

We must point out that the above scenarios and hypothesis are not necessarily mutually exclusive. The ecological scenario of any one species is a multidimensional space, and many pressures affect species at the same time. Resource availability, predation risk, direct and indirect fitness costs, and kin selection, all these pressures are summed, and may compound or mitigate each other's effects on the positive or negative selection of group living. If we are to explain sociality on different species, we must look at all these causes at the same time, and weigh their effects to find the most likely explanation(s).

2.2 Social cognition and memory

We have seen a few explanations of how animals come together, and now we will explore a bit what happens when they do. Though, as we saw above, interaction is not needed for group formation and maintenance, they open new pathways for the animal to take. One such pathway is that of social cognition. According to Seyfarth, Cheney, and Longo (2015), social cognition is "knowledge about conspecifics". This knowledge implies that animals can, to a certain degree, recognize each other and store information about them. This can have enormous implications inside a group. These implications are what guide the work we present in the next chapters. Here, we will review a little about how this recognition works.

2.2.1 Types of recognition

Given that groups are formed and maintained, by any of the above mechanisms, we must ask: can animals know which others are members of their group and which are not? Can animals recognize and differentiate between each other? Is there an advantage to knowing your peers?

Friend or foe?

Familiarity comes in different levels. There is this sort of "I have seen that guy before" we experience when we go to have lunch every day at the University Restaurant for years, seeing the same people at the same time of day, there is this intimate knowledge we have about the people with whom we share our houses, and there is a whole spectrum in between. To become familiar with an individual means to learn a set of traits that can be used to distinguish the individual from a set of others. Those traits do not necessarily need to be facial or body features unique to each individual. Sports fan can readily identify and bond with others who wear their team's colors and symbols, irrespective of whether they have seen each other before, and sometimes

they even antagonize those wearing their rival teams colors. Likewise, a general marker can be used by animals to identify their conspecifics. Ants do not recognize each and every other ant inside the nest, but they recognize a colony scent, a pheromone shared by all those who live in the same nest, and quickly attack those who enter their nest with a different scent (Lenoir, D'Ettorre, and Errard 2001), and burrowing mammals use scent to discriminate nestmates from strangers (O'Riain and Jarvis 1997). This type of familiarity is called *Class-Level Recognition* (CLR, Tibbetts and Dale (2007)). CLR is a quick and effective way of assessing a conspecific, and is probably the most common form of recognition. Though this most general recognition can sometimes be enough, recognition can also be more fine-grained. Animals can have several "internal categories" which they can use to classify their conspecifics. The other can be classified a mate, a subordinate, a neighbor, a dominant, or a rival. The number and specificity of these categories can vary according to the species' ecological and physiological constraints (Gherardi, Aquiloni, and Tricarico 2012).

Some degree of CLR has been demonstrated across the animal kingdom (*e.g.* birds (Godard 1991), mammals (Johnston 2003), crabs (Detto et al. 2006), and lobsters (Karavanich and Atema 1998)). CLR is sufficient to maintain hierarchies in some species (Gherardi 2005): it is not necessary to recognize who is the alpha⁷ precisely, only to be able to know that it can beat you in a fight. It has been shown even for solitary animals. Individuals that defend territories can recognize their neighbors, and act differently towards them than towards strangers. When this difference is an apparently reduced aggression level, it is called the *dear enemies* effect (Temeles 1994), but the opposite, increased aggression towards *nasty neighbors* (C. A. Müller and Manser 2007) has also been observed. This does not imply that territory neighbors are capable of differentiating between neighbors, but they certainly can differentiate between neighbors and strangers. To be able to truly differentiate between individuals requires a higher degree of specialized memory, Individual Recognition.

Individual recognition (IR) is the most specific form of recognition: the animal appears to have an internal representation of another individual, with which a set of memories is associated. This opens the way for quantitatively and qualitatively different relationships between individuals, due to the possibility of repeated interactions having history-dependent outcomes. We examine

⁷**Alpha:** the dominant individual in a group. Traditionally in vertebrates, especially in species with linear hierarchies, individuals are designated by greek letters according to their place in the hierarchy.

IR and its consequences for sociality in more detail in chapters 3 - Recognition And Sociality and 5 - Do I know you?

2.2.2 Reciprocal altruism

Recognition opens the way for one of the most studied types of interaction, reciprocated altruism. We have seen how altruism can appear in a selfish world, but reciprocated altruism takes the benefits one step further: if interactions can be repeated between the same pair of individuals, then benefits can compound like interest. Long lasting alliances can be formed, and cheaters can be punished. As we will see in section ??, cheaters always have the fitness advantage if interactions are one-shot. If animals can remember past interactions, then cheating stops being advantageous, and cooperation strategies gain ground, as animals can now choose not to cooperate with cheaters again.

2.3 A model of social interaction as a driving factor of group formation

We have seen how external pressures like predation or resources can influence grouping. In this work, we will not concern ourselves here with those pressures. Rather, we will focus on the effects of a particular internal factor, social recognition, on the formation and structure of groups. Interactions, specially if they have movement consequences, can alter a group's spatial and social structure. It is to be expected that a group with many interactions will have a different social network than one created by selfish herd reasons. It is also to be expected that, given the same external conditions, if affiliative interactions are strong, the group will be comparatively more compact than a random assemblage of conspecifics, and that some individuals will be removed from the group due to agonistic interactions.

2.3.1 Social Behavior definitions

In box 2.2 we state the definitions of social behavior terms that we will be using on the next chapters of this thesis. We will use these basic definitions to create a model of social memory to investigate its effects on group formation and structure

We choose to define groups here purely on a spatial basis to avoid any implications that can come with a behavioral-based definition, such as communication, hierarchy, or even kinship. Animals can group for various reasons, and to restrict our definition of group to depend on

communications would be counter-productive to our objectives. Calling an aggregation of individual caused by spatial constraints a group can seem counter-intuitive when dealing with behavioral questions, but it allows us to examine a broader range of situations, and to compare them.

We also chose to define the different types social behaviors based purely on movement, to reflect our definition of group. By our definition, animals can form groups based on random movements, but affiliative behaviors cause individuals to move closer more often, and therefore, cause groups to last longer, and the opposite holds for agonistic behaviors. Thus, mating and food-sharing are affiliative behaviors, in that the proximity they cause is long lasting, and a fight is considered an agonistic behavior because, while it brings individuals together for the duration of the event, it is safe to say that at least one of the animals will leave the area afterwards, especially in territorial disputes. We expect that the additive effects of social behaviors will cause groups to show a different structure than that of groups created solely by random movement. We separate affiliative behaviors from agonistic ones due to the fact that a decrease in affiliation not necessarily leads to an increase in aggression, and it allows us to in the future extend the model to include the effects of variation in sociality into our analysis.

All behaviors that do not affect the group directly are lumped together as neutral behaviors. Neutral behaviors can bring individuals closer together or drive them apart, but this proximity is not derived from interaction, and therefore not social under our definitions. As our definition of group is not based on social interactions, neutral behaviors can give rise to groups, but it is expected that these groups will be short-lived, as the non-interacting individuals go about their businesses. These definitions may seem like oversimplifications of complex phenomena, and it would certainly be more realistic to add gradations to the intensity of each type of behavior, but doing so would add unnecessarily complexity to the model. A simple affiliative / agonistic / neutral classification of behaviors allows us to compare situations with and without memory without worrying about the effects of affiliation or aggression levels, or the external causes of these behaviors. Though these definitions are rather loose, and certainly not a consensus, they are useful and sufficient for our purposes, as they avoids biases towards “socio-positive” behaviors such as allogrooming and mating, and include aggressive behaviors, which are usually not seen as “social”, but can certainly affect a group’s structure and stability.

2.3.2 Memory

For our purposes, social memory can be broadly defined as an animal's internal representation of a collection of learned facts and interactions related to a conspecific. This implies that social memory is a multidimensional entity, encompassing several traits and situations, which changes throughout the individual's life. Since we are only interested in the effects of social memory, and not its causes or nature, we represent this multidimensional entity as a simple sequence of social behaviors. We are specially interested in individual recognition (IR), and in Chapter 5 - Do I know you? we investigate how IR affects group size, number of groups and group stability.

Box 2.2 — Terms and definitions of social behavior and memory.

We purposefully avoid using terms like society, colony, band, flock, and others as they are loaded with meaning, and can imply a defined group structure.

- **Group** - *A spatial aggregation of conspecifics, regardless of presence or absence interactions between the individuals it comprises. We choose to use a purely spatial definition as we study here the effects interaction have on grouping, and including interaction directly on the definition would have been troublesome.*
- **Group structure** - *The pattern of social behaviors between individuals in the group.*
- **Group stability** - *Group persistence through time.*
- **Social behaviors or Interactions** - *Any interaction between two conspecifics.*
 - **Affiliative behaviors** - *Social behaviors which tend to increase grouping.*
 - **Agonistic behaviors** - *Social behaviors which tend to decrease grouping.*
 - **Neutral behaviors** - *Behaviors that do not involve interaction with other conspecifics directly.*
- **Memory** - *An individual's internal record of its previous interactions (social behaviors) with other conspecifics. We will use the terms **memory** and **social memory** interchangeably.*
- **Recognition** - *The ability to discriminate between familiar and unfamiliar conspecifics - Recognition does not imply the ability to differentiate between two different familiar individuals, only to recognize a particular cue as known or unknown (for instance, a particular colony odor).*
- **Individual Recognition (IR)** - *The ability to associate a particular memory with a particular recognized conspecific.*

3 — Recognition And Sociality

Abstract

Individual recognition is a widely studied phenomenon in animal behavior, with several consequences for the social structure of a species. When we say that an individual recognizes conspecifics, we mean that it is actually capable of discriminating between conspecifics in terms of individual identities, rather than merely discriminating between classes of individuals such as “neighbor” or “mate”. Current investigation paradigms for individual recognition rely on exposing an individual to a conspecific, then assessing its behavior on a subsequent re-exposure. Experiments aiming to explore individual recognition have to be well designed to avoid confusion between class-level and true individual recognition. However, most present studies suffer from design problems and cannot properly differentiate between the two phenomena. We propose using information from the neurobiology of social behavior and simulations to overcome some of the problems with current experimental designs. Social recognition is based on the neurological substrate of memory formation and retrieval, and is specially influenced by the nonapeptides oxytocin and vasopressin and their respective non-mammalian homologues. Information from the distribution of nonapeptide receptors and the effects of nonapeptide infusion on social memory can be used to guide the design of recognition experiments, and comparative approaches can be used to study the evolution of social behavior. Individual-based simulation and game theory serve as a means to propose and test hypothesis about individual recognition, by generating expected patterns of social behavior based on proposed mechanisms of interaction, patterns that can then be compared to those observed in nature in order to test hypotheses and design robust experiments. By using currently available techniques, behavioral biologists can design experiments that are more robust in order to investigate social recognition and its related phenomena.

3.1 Introduction

Group-living presents a series of advantages to the individuals, together with a series of disadvantages (Davies, Krebs, and West 2012; Sheehan, Straub, and Tibbetts 2014). However, how can individuals tell who is part of the group from who is not? For some kinds of groups, such as the selfish herd described by Hamilton (1971), the composition of the group is of little importance. On the other hand, there are species that are very strict about who is part of the group. Honey bees, for instance, will attack any bee entering the hive which does not have the appropriate colony odor (Breed 1998). In some species, a strict hierarchy exists inside each group, with individuals knowing their place and that of their partners (*e.g.*, Aquiloni and Gonçalves 2012; Bergman et al. 2003; Moolman, Bennet, and Schoeman 1998). Altruistic behavior, particularly reciprocated altruistic behavior, depends on individuals not only recognizing one another, but also remembering how they have previously behaved toward each other. For instance, vampire bats (Carter and Wilkinson 2013) are more likely to share meals with bats who have shared meals with them before. In order to distinguish between conspecifics, individuals must be able to recognize some distinctive quality about their conspecific, and to react to this quality in some way, be it to recognize relative dominance status or simply to discriminate "familiar" versus "non-familiar" (Mateo 2004; Thom and Hurst 2004; Tibbetts and Dale 2007). These general types of recognition are usually termed class-level recognition or social recognition. We will use the terms interchangeably to distinguish general recognition from true individual recognition. True individual recognition, while it can be evident in some groups, such as primates, is rather hard to separate from these more broad types of recognition (Gherardi, Aquiloni, and Tricarico 2012; Mateo 2004; Wiley 2013). Here, we will review some of the evidences and mechanisms associated with individual recognition and its relation to memory formation in several different animal groups to shed some light on the role of individual recognition in the evolution of sociality and group formation.

3.2 Individual recognition

When we say that an animal subject recognizes a conspecific, we mean that it is reacting to a trait or set of traits the conspecific possesses. The specificity of this association can vary greatly, from a mere yes/no familiarity to true individual recognition. In individual recognition (IR), the

individual doing the recognition (the receiver) needs to be able to (i) perceive and learn a certain phenotypical trait (known as cue) of the individual being recognized (the emitter), and (ii) to distinguish that trait from those of other conspecifics (Thom and Hurst 2004), which implies a sophisticated sensory and memory system. Some degree of IR has been demonstrated in several different animal groups, including mammals (Briefer, Padilla de la Torre, and McElligott 2012; Bruck 2013; Insley, Phillips, and Charrier 2003; Johnston and Bullock 2001; Mateo and Johnston 2000; O’Riain and Jarvis 1997), birds (Akçay, Wood, et al. 2009; Godard 1991), wasps (Sheehan and Tibbetts 2008), octopuses (Tricarico et al. 2011), mantis shrimps (Caldwell 1985), salamanders (Kohn et al. 2013), and frogs (Bee and Gerhardt 2002). In contrast, class-level recognition (Mateo 2004; Tibbetts and Dale 2007; Wiley 2013) involves much less investment, requiring only that a conspecific be assigned to a certain group, such as mate, offspring or colony-mate.

Whether an individual can truly distinguish different individuals from each other based on individual specific traits, or merely recognize that a conspecific falls within a certain category of individuals, can be rather difficult to ascertain, even in controlled experimental settings (Tibbetts, Sheehan, and Dale 2008; Wiley 2013). Tibbetts and Dale (2007) propose that for true individual recognition to occur, (i) the emitter’s cue, (ii) the receiver’s internal template, and (iii) the receiver’s behavioral response, all must be individual-specific. The latter two are extremely difficult to differentiate from class-level templates and reactions, as highlighted by Steiger and J. K. Müller (2008) in a critique to Tibbetts and Dale (2007) (see also the review by Wiley 2013). For instance, in monogamous species or those with single offspring, it can be impossible to tell whether an individual can differentiate between "mates" or "offspring", as those classes are formed by single individuals. Even in cases where individuality in a cue can be detected by researchers, the individual does not necessarily use that cue to recognize conspecific individuals (*e.g.*, Budka and Osiejuk 2014; Hale, Nelson, and Augustine 2014). To understand why it is so difficult to differentiate between class-level and true individual recognition, we will now examine how IR is identified and tested.

3.2.1 Identifying and testing IR

The standard way to test for IR, known as the social discrimination paradigm, is to pair unfamiliar individuals for a given familiarization period (Ferguson, Young, and Insel 2002; Kooij and Sandi

2012; Thor and Holloway 1982), allowing them to establish dominance relationships, if that is the case for the species. The individuals are then moved to different enclosures, and after some time the focal individuals are presented with either unfamiliar or familiar individuals, or their individual cues, such as scents or recorded callings. The appropriate behavioral measurements are taken, and it is expected that if IR exists, individuals will react differently to known conspecifics by exhibiting fewer aggressive behavior or performing affiliative behavior towards them, such as allogrooming (mutual cleaning). However, for true IR to be identified, the focal individual must show discrimination not only between familiar and non-familiar conspecifics but also between known individuals. Another common experimental situation is to present an individual with both a known and an unknown conspecific individual in opposite sides of the same enclosure, called the social discrimination test (Ferguson, Young, and Insel 2002; Kooij and Sandi 2012). It is assumed that if IR exists, the focal individual will move towards the known individual or perform aggressive displays against the unknown individual. Both these experimental setups, however, have problems in separating class-level from individual recognition if the experiments are not well designed. This means that the experimenter must be careful to design it in such a way that it is possible for the test animal to discriminate between different known individuals, not only between known and unknown ones. More than that, depending on the behavior being observed, the recognition can be masked. For instance, yellow-bellied tit males (*Parus venustus*) and corncrake males (*Crex crex*) do not show differences in vocalization responses to calls from strangers, but do show differences in other aggressive behavior (Budka and Osiejuk 2013; Wei, Lloyd, and Zhang 2010). In another work, Gherardi, Aquiloni, and Tricarico (2012) reviewed the evidence for individual recognition in invertebrates and have identified 10 species with the best evidences for individual recognition. However, the authors stress that most tests have not investigated all components of IR, especially the specificity of clues and plasticity of individual templates and template matching.

To identify true IR, first it is necessary to isolate the cue that the individuals use for recognition, and then to determine whether that cue is individual-specific. Once an individual-specific cue is identified, it is necessary to investigate whether the receiver acts differently in response to such cues (for instance, the conspecific itself or a tissue with the conspecific's odor) from different known conspecifics. If all three conditions (cue is used for recognition, cue is individual-specific, and the receiver reacts differently to cues from known individuals) are met, the species can be

said to have individual or class-level recognition, Even though this "recognition of familiars" may seem to be a case of true IR, it is not necessarily so. The receiver can be merely reacting to a familiar cue, such as a song or scent, but does not necessarily need (or is able to) to remember and differentiate between specific individuals (Wiley 2013). Additionally, individuals may be simply responding to a perceived threat level, regardless of actual familiarity (Booksmythe, Jennions, and Backwell 2010). In these cases, the recognition would be a class-level response, rather than true IR. An experiment can be designed in which that cue is manipulated, for instance, by painting facial markings as Tibbetts (2002) has done with wasps, or by dousing an individual with another's odors. If the individual responds differently to a known conspecific whose cue has been altered, then true IR can be said to exist. Indeed, (Tibbetts 2002) has shown that *Polistes fuscatus* wasps decrease aggression against wasps whose face markings were altered as they become familiarized with them, reinforcing the notion that individuals of this species are indeed capable of individually recognizing conspecifics by their facial markings and learning new cues.

Recognition, be it true IR or class-level, is dependent on memory, particularly long-term memory; and memory formation, consolidation and retrieval is particularly affected by some neurotransmitters and hormones. The levels of these hormones and neurotransmitters can be manipulated to gain insight about the mechanisms involved. In the next section we will look at long-term memory of social interactions, and how it is regulated. Since most papers do not investigate individual recognition *per se*, we will also review work done on social recognition.

3.3 Social recognition and the neurology of social memory

In nature, social memories can last for a long time, sometimes even decades after separation, particularly in long-lived species. For instance, bottlenose dolphins (*Tursiops truncatus*) can recognize conspecifics after as much as 20 years of separation (Bruck 2013). Female goats (*Capra hircus*) recognize offspring calls for more than a year after weaning (Briefer, Padilla de la Torre, and McElligott 2012). Some species of pinnipeds show mother-offspring recognition for 2-3 years (Insley, Phillips, and Charrier 2003). Ravens (*Corvus corax*) modulate their calls differently in response to familiar individuals met up to three years in the past (Boeckle and Bugnyar 2012). Invertebrates can also show proportionally long-lasting memory: Polistine wasps (Sheehan and Tibbetts 2008) show IR after a week of separation and several encounters with other conspecifics, and lobsters (*Homarus americanus*) can recognize previous opponents for up

to two weeks after an encounter (Karavanich and Atema 1998).

There is also evidence that not all social memory is of long-lasting nature. Belding's squirrels (*Spermophilus beldingi*) have the ability to recognize familiar kin, but not familiar non-kin individuals after hibernation, which shows that, in some species, some sorts of individual recognition can be affected by time (Mateo and Johnston 2000). In laboratory rats, handling the individuals between encounters results in investigation of the conspecifics not being reduced, implying decreased social recognition of familiars (Burman and Mendl 2000), which indicates that in some species, a long exposure is necessary to consolidate long-term memory of individuals. Long-term memory consolidation is dependent on several factors (Nadel et al. 2012), but it has been shown to be enhanced by the effects of nonapeptides, a class of neurotransmitters which have been strongly linked to memory and social behaviors, both in vertebrates (Stoop 2012) and in invertebrates (Gruber 2014), and by gonadal hormones in vertebrates (Gabor et al. 2012).

Nonapeptides are important mediators of social behavior in both vertebrates and invertebrates. The two main nonapeptides implicated in social behavior are oxytocin and vasopressin, and their non-mammalian homologs. These signaling molecules have their structure strongly conserved throughout the animal kingdom, and receive various names depending on the groups in question. They are involved in a host of social behavior, such as pair bonding and parental behavior, in several groups (Donaldson and Young 2008; Gruber 2014). We will focus here on the effects of oxytocin (OT) and vasopressin (AVP), as they are the most studied ones.

Oxytocin-knockout mice, that is, mice which do not express the OT-producing gene, show greatly impaired social functions, and have been shown to not form social memories (Ferguson, Young, and Insel 2002), and to fail in social discrimination tests (Choleris et al. 2006). Conversely, infusion of OT in normal rats has been shown to preserve social recognition for longer periods (Dluzen et al. 2000). In a review, Gabor et al. (2012) suggest that OT is involved in the formation, rather than retrieval or consolidation of social memories.

Vasopressin / vasotocin (AVP/AVT, also known as Anti-Diuretic Hormone, or ADH) is another important neurotransmitter that has been linked to memory formation. AVP- deficient rats show consistent problems in memory formation (van Wimersma Greidanus 1982), and administration of AVP has been shown to prolong social memories in male rats (Sekiguchi, Wolterink, and Ree 1991). The distribution of AVP receptors has been shown to be quite different in species with different levels of sociality, including closely related species (Insel, Wang, and

Ferris 1994) and even in individuals of the same species. In the vole *Microtus ochrogaster*, for instance, individual variation in the expression of the vasopressin receptor V1a serves as a predictor of individual variation in social behavior (Hammock and Young 2005; Ophir, Wolff, and Phelps 2008), with individuals that express more of the receptor showing increased social behavior. In an experiment with two related species of vole, one solitary (*M. montanus*) and one that forms long lasting pairs (*M. ochrogaster*), Young et al. (1999) changed the V1a receptors in the brain of the solitary vole to those of the social one. The transgenic solitary voles expressed receptor patterns similar to those of social ones, and exhibited increased social behavior when injected with AVP. In mice, Bielsky et al. (2005) showed that the V1a vasopressin receptor is deeply involved in social cognition, and that its overexpression in wild-type mice increased recognition time of conspecifics from half an hour (in untreated mice) to 24 hours after the initial encounter. In *Polistes metricus* wasps, Toth et al. (2007) found that the gene expression pattern in the brain of workers, which care for the brood, is similar to that of colony foundresses, which also care for the brood before becoming queens. Queens and gynes (females that will found future colonies) of this species, both of which do not show maternal behavior, also have similar patterns of gene expression, different from that of workers and foundresses. These results show gene expression patterns are also important in determining social behavior among invertebrates. Both OT and AVP are important neuromodulators, and their receptors are expressed in several different areas of the brain, including the hippocampus, where they may have a role in memory formation and retention, but their effects vary wildly between brain areas, and can sometimes be difficult to separate.

Social recognition in rats and mice has also been shown to be highly affected by gonadal hormones (Bluthé, Gheusi, and Dantzer 1993; Gabor et al. 2012; Gheusi et al. 1994). In male rats, castration impairs social recognition in male rats, which can be reversed by testosterone implants (Bluthé, Schoenen, and Dantzer 1990; Thor, Wainwright, and Holloway 1982). In ovariectomized female mice, long term social recognition is absent, but can be reversed by estrogen replacement therapy (Tang et al. 2005). Estrogen-receptor knockout mice also show impairments in social recognition tests, even with their OT and AVP receptors intact, and it has been shown that estrogen receptor- α and OT are necessary for social discrimination and individual recognition (Choleris et al. 2006). There is also evidence that short-term social memory in female rats is affected by narrow fluctuations in endogenous oxytocin during the

estrous cycle (Engelmann et al. 1998). Now that we have seen a little about the neurology of social recognition, we will take a brief look at how the knowledge of the differences in social recognition can be used to study its consequences on animal's lives, especially its effects on cooperation.

3.4 IR and cooperation

One important consequence of memory and recognition is that they allow for repeated interactions between individuals to have cumulative effects, allowing for phenomena like altruistic behavior and cooperation to emerge. (Hamilton 1964b), for instance, has shown how cooperation between kin can be selected for: altruistic behaviors are selected whenever their gain in fitness (direct or indirect) is greater than their cost. IR is not necessary for cooperation to occur between highly related individuals, as honey bees show no sign of recognizing individual workers or drones, instead recognizing a colony scent and reacting against those with different scents (Breed 1998), but all evidences show that some degree of recognition is necessary for cooperation between unrelated individuals. Social cognition, be it true IR or class-level recognition, opens the door for cooperative behaviors if the same individuals interact repeatedly, regardless of whether they are related or not (Carter and Wilkinson 2013; Dugatkin 2002; Mesterton-Gibbons and Dugatkin 1992; Trivers 1971) . This has traditionally been studied by means of game theory. Game theory allows us to model how an individual makes decisions, and the outcome of those decisions in terms of fitness payoffs. The best known application of game theory to animal behavior is the prisoner's dilemma (Clements and Stephens 1995).

In the prisoner's dilemma, two individuals can choose independently to cooperate towards a goal (for instance, reproduction or foraging) or to defect. Each individual stands to gain a certain amount if they both cooperate, and to gain very little (but still something) if they both defect. If one defects and the other cooperates, the defector takes all and the cooperator gains nothing. Thus, in a single game, the best strategy for an individual is to defect, which ensures a minimal non-zero payoff if both defect and a maximal payoff if the other player cooperates. Applied to individual interactions, this seems to be a barrier for the evolution of cooperation because cooperators would quickly be selected against and removed from the population due to their fitness loss, as the cheater's payoff is always greater than that of the cooperator. However, that is only true if the individuals only interact once or if they cannot remember previous interactions.

If the game is played repeatedly with the same partner, things change. The best possible strategy becomes to cooperate on the first turn, then to repeat your partner's strategy on the previous round. This strategy is known as the tit-for-tat strategy and it is the simplest kind of reciprocity (Axelrod and Hamilton 1981). Using game theory simulations, Axelrod (1984) has shown that tit-for-tat is the best possible strategy for an individual, and it allows reciprocity and cooperation to arise under different scenarios (Nowak 2006). It has been observed in several animal groups, but is by no means the only strategy seen in nature, see Doebeli and Hauert (2005). Carter and Wilkinson (2013), for instance, showed that food sharing in vampire bats is strongly correlated with reciprocity, even in unrelated pairs. In several species of primates, reciprocity is also a better explainer of allogrooming than kinship (Schino and Aureli 2010). Finally, when zebra finches (*Taeniopygia guttata*) are paired with a known partner, i.e., when they can expect future repeated interactions, they maintain higher levels of cooperation than when paired with one-off partners (St-Pierre, Larose, and Dubois 2009). Even though strict tit-for-tat is played only by two individuals, some species can use indirect evidences of cooperation with a third party, a phenomenon known as eavesdropping, to determine whether to cooperate or not. For instance, males of the song sparrow *Melospiza melodia* can perceive when a neighbor intrudes on another neighbor's territory, and act in retaliation against the trespasser (Akçay, Reed, et al. 2010). Green swordtail fishes (*Xiphophorus helleri*) can perceive whether a conspecific has won or lost an aggressive encounter against a third fish, and adjust their propensity to fight accordingly (Earley and Dugatkin 2002), diminishing the probability of attacking a winner or a particularly aggressive loser.

It is not possible to directly access an individual's inner cognition processes, that is, to know exactly how they make their decisions and what they take into account to choose a strategy. However, we can use simulations in which individuals and their behaviors are explicitly modelled (known as Agent-Based Models, or ABMs, see Grimm and Railsback (2005)) to create possible scenarios and decision rules. This allows us to model how individuals should behave if they had different levels of sociality, memory, and individual recognition. This approach to studying IR differs from game theory in that the individuals' behaviors are explicitly modelled, instead of just the fitness payoff of their strategies. This type of virtual experiment can offer a window into an individual's cognitive processes: by explicitly modelling the animals' behaviors, we are spelling out our models of their decision processes, and the kinds of information on which we believe

they base those decisions. This allows us to make predictions based on those models (e.g., group size, frequency of affiliative behaviors, social network structure). The patterns that emerge from these ABMs can be compared to those of real species, a technique known as pattern-oriented modelling (Grimm, Revilla, et al. 2005; Zurell et al. 2010). Even though it is not possible to be sure whether the rules implemented by the model are the ones actually used by the individuals, the models can be used to generate predictions and hypotheses about social behavior that can be compared with natural situations (Vaart and Hemelrijk 2012; Wiegand et al. 2003).

For instance, Hemelrijk (2000b) has created an ABM to study dominance interactions in primates. In her model, the individuals can perceive their relative dominance status to each other and engage in dominance interactions, leading to a hierarchically structured society. This allowed her to investigate the emergence of a spatial structuring often observed in primates, where the dominant individuals sit at the center of the group. (King et al. 2011) have modelled the dynamics of collective movement in desert baboons (*Papio ursinus*), testing a few different decision rules, which they derived from real-world observations. They successfully identified a simple decision rule, based on individuals following those with whom they have higher association, which replicated the real-world observed pattern in the simulations. This helped to understand the social dynamics of the system in question. Puga-Gonzalez, Hildenbrandt, and Hemelrijk (2009) have created a model of hierarchical social interactions between macaques (*Macaca* spp.), which was capable of reproducing social patterns found across several species, and which Beltran and Dolado (2012) subsequently used to generate and test hypotheses about the social structure of a different species, *Cercocebus torquatus*.

These modelling approaches (ABMs and game theory) should take into account the mechanisms of social and individual recognition. When investigating the evolution of individual recognition, for instance, one could model it as a strategy under the game theory framework, to assess under what conditions it is positively selected, or use ABMs to investigate how changes in degrees of social recognition can affect the structure of groups.

3.5 Conclusions and perspectives

Recognition and memory play a great role in individuals' social lives, ranging from partner choice to within-group hierarchy. Though many species are said to be capable of some degree of IR, true IR is probably rare (Wiley 2013). This could be because memories are stored in

neural tissue, a metabolically expensive tissue (Herculano-Houzel 2011), and therefore it is not a stretch to assume that memories are expensive as well. Indeed, Mery and Kawecki (2005) have shown that long-term memory formation in *Drosophila* has a metabolic cost that can reduce life expectancy in starvation conditions. We are not aware of similar study that show such extreme costs in vertebrates, but the costs for neuronal spikes are known to be considerably high (Lennie 2003), thus we should expect to see true IR only when it yields a significant gain in fitness.

Even though IR has received considerable attention in recent years, there are important questions to be addressed, such as how common true IR is, how it can evolve from class-level recognition, what (if any) are the neurological differences between species showing one or the other, and what advantages it has that can cause it to become fixed in a species. However, approaching these questions is difficult, because present experimental paradigms have trouble differentiating true individual-level from class-level recognition, as Gherardi, Aquiloni, and Tricarico (2012) show in a review of social recognition in invertebrates. Most experiments are not explicitly designed to discriminate between different known individuals of the same class and it can be impossible to know directly how (or even if) the receiver compares different senders (Gherardi, Aquiloni, and Tricarico 2012; Mateo 2004), further complicating matters. There are, however, ways to overcome these problems.

Well-designed experiments are the most direct approach. Designs which test whether the receiver reacts in a specific manner different known senders, and not to just any kin or nest-mate (*i.e.*, controlling for kin/group recognition), or to just any larger or smaller known conspecific (*i.e.*, controlling for status recognition via signalling), can be used to indicate true IR, as exemplified by Gherardi, Aquiloni, and Tricarico (2012). These experiments should also be designed to investigate multiple behavioral responses of the receiver, given that species can react to conspecifics via multiple behaviors, and the response may not be perceived when looking at a single behavior (*i.e.*, the corncrakes responding to invader calls via threatening postures but not via singing, see Budka and Osiejuk (2014); Wei, Lloyd, and Zhang (2010)). The ideal experiment would investigate a cue which (i) is individually specific to the sender, (ii) is used for recognition and (iii) causes the receiver to act in a manner which varies according to the identity of the sender.

These experiments can also be enhanced by comparing related species, which can shed light on the evolution of social behavior, via traditional experiments, as Sheehan, Straub, and

Tibbetts (2014) have done with *Polistes* wasps. Comparative neuroendocrinology approaches can also be used to better understand the evolution of social recognition. By examining the patterns of expression of nonapeptide and hormone receptors or genes in an individuals' brain, and comparing it to that of a closely related species with a different social system, it is possible to assess how sociality might have evolved, since differences in these patterns are indicative of differences in social behavior, in both vertebrates (Insel, Wang, and Ferris 1994) and invertebrates (Toth et al. 2007). This approach, together with an understanding of the ecology of the species involved and molecular phylogeny data, can be used to map the evolution of sociality in a given group.

The experimental approach can also benefit from the recent advances in simulations and game theory. Although examples of hypothesis generation and testing using simulations in animal cognition research are still scarce, and few of those which exist include any sort of memory on their models, (e.g., the knowledge of relative hierarchy positions in the DomWorld of Hemelrijk (2000a), the papers mentioned in this review illustrate how simulations can be used to generate and test hypothesis about social systems. When combined with techniques such as social network analysis, and spatially explicit models, these kinds of simulations can be powerful tools to study the effect of recognition and social memory in group formation and dynamics. Social network analysis (for instance, (Krause, Lusseau, and James 2009; Lusseau and Newman 2004; Sueur et al. 2011) allows us to investigate the social interactions of the real animals, *e.g.* how they are divided in subgroups, what are their patterns of reciprocity and hierarchy structures. Researchers can propose mechanisms by which these patterns and structures are generated via individual interactions, and test whether these mechanisms generate in the simulations the same patterns observed in nature, as (King et al. 2011) did for the desert baboons. The same holds true for spatially explicit models ((Fagan et al. 2013; Shaw and Couzin 2013), as Hemelrijk (2000a) has shown by demonstrating the emergence of a spatially structured group based on dominance interactions.

Game theory in particular has already been used extensively to model and understand social phenomena, and has helped shape our current understand of the evolution of cooperation and social behavior in general (Doebeli and Hauert 2005). Game theory can show how a strategy such as cooperation can become fixed in a species if it provides a gain in fitness. This can be one explanation as to why true IR is rare. If IR is so costly as some believe it to be Wiley (2013),

for instance, compares it to the complexity of language), one can expect it to rarely become fixed, except in cases where it offers a significant advantage. Recently, research on game theory has moved from the traditional repeated dyadic interactions to spatially explicit games, where patterns of cooperation and defection can emerge depending on the spatial configuration of the players (Doebeli and Hauert 2005; Nowak, Bonhoeffer, and May 1994), and the topology of their social interactions (Killingback and Doebeli 1996; Lieberman, Hauert, and Nowak 2005; Ohtsuki, Hauert, et al. 2006; Ohtsuki and Nowak 2006). A natural extension of this would be an iterated game in which the topology of interactions is not fixed, *i.e.*, a game between moving individuals who interact with others in a certain radius, as in the individual-based schooling and flocking models. However, as far as we know, this has yet to be done. This kind of spatially explicit, individual-based, game-theoretical approach is closer to how animal societies actually work, which allows a broad range of scenarios to be tested. This allows social phenomena other than cooperation/defection to emerge, such as fission-fusion societies or hierarchies, depending on the rules implemented.

By themselves, the above techniques, experimental design, neurobiology and individual-based modelling, are powerful enough to warrant their individual uses, but taken together they are invaluable assets to advance the study of individual recognition and social memory. It is not necessary (and in some cases may be unfeasible or undesirable) for a single study to use all of them together, but when designing recognition or memory experiments, for instance, it is useful to have in mind the neurobiology of the species in question. Whether the individuals actually recognize differences in the social cues being tested, what is the correct exposure time for memory consolidation, whether that memory is susceptible to interference by other social encounters, how the focal individual reacts to the cues of the emitter being altered, or if the individuals use multiples cues to identify other individuals, all of this should be taken into account in the experimental design, and these questions can be answered by neurobiological approaches. Simulations can also aid in the design of experiments by generating null hypothesis and predictions about the patterns one can expect to see, or even by testing different competing hypotheses about internal cognition mechanisms that cannot be accessed by other means, but that should result in different observed patterns. In recent years, there have been great advances in these tools, which are readily available for behavioral biologists, and future studies should aim to use them to the best of their possibilities.

4 — Modelling choices

4.1 Social memory simulator

We chose to approach our main questions using a modelling technique called agent-based modelling. The ODD protocol was created by Grimm, Berger, et al. (2010) to be a straightforward way of conveying a model in terms that would allow its reproduction. The full ODD description of the model is presented in the next chapter, section 5.7. The protocol is relatively successful, but it does not necessarily contain the reasoning behind the modelling decisions made, which we believe are as important as the model itself, since they are the premises upon which the model is built. Thus, in this chapter, we will explore in greater detail the reasoning behind our modelling decisions, the techniques we used, and the impact they have on the model results, to serve as an introduction to agent-based modelling. We will not dwell in programming details, as they are language-specific, except in the rare cases where they are relevant to specific choices that have to be made in order to proceed with model-building.

4.1.1 Agent-based models

Agent-based models (ABMs, Grimm and Railsback 2005), also called individual-based models, are uniquely suited to problems where individual variation is key. In this type of model, entities such as individuals are represented as agents. This allows each individual in the model to have unique histories and behaviors, which means that each agent can have, for instance, its own genetic code Martins, Aguiar, and Bar-yam (*e.g.*, 2013)), or its own perception of the world,

which allow for emergence of macroscopic properties from microscopic mechanisms (Grimm, Revilla, et al. 2005). ABMs allow for agents to represent individuals of different species, with differing ecological traits and resource requirements. ABM are also well-suited to investigate mechanistic models, by representing entities with defined interactions and internal processes. Agent-based models have successfully been used to model certain aspects of animal societies, like hierarchies. Hemelrijk (2000a) used an ABM to model the hierarchy of a group of primates based on agonistic interactions, in which individuals had an internal model of their positions in the overall group hierarchy. These kinds of characteristics would be extremely difficult to model with traditional mathematical tools, which are more suited to homogenous entities with regular behavior.

Box 4.1 — Agent-Based Modelling terms and definitions.

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- **Agent** - *A computational representation of an individual with its own behaviors and qualities.* Each agent has a memory, which is a list of its previous encounters with other agents
- **Actor:** the focal individual, the one who does the action.
- **Co-actors:** the other individuals in the the actor's neighborhood, the ones receiving the actions
- **Neighborhood or Interaction radius:** the maximum distance in which an actor can perceive other agents and the world.
- **Object-oriented language:** A programming language which can represent the modelled entities in the form of objects with their own variables and functions, that can be used to represents traits and behaviors of agents.
- **Debugging:** The act of looking for and correcting errors in the code .

■

Programming language

There are many programming languages suited for ABMs, and some, such as NetLogo (Willensky 1999), were designed specifically for that purpose. Any object-oriented language would be suitable for ABM's, but successful ABMs have been built in languages like FORTRAN (Martins, Aguiar, and Bar-yam 2013) or R. An important feature to consider when writing the code is that it be platform-independent, so that the model can be run on any operating system without change. We chose to build our model using C++11 instead of other programming languages such as NetLogo due to its low computer memory requirements and the powerful debugging tools available. Computer memory was a requirement because we needed to represent the individual

histories of thousands of agents for thousands of rounds, and a good debugger is always a good thing to have. The choice of language can also depend heavily on personal preference and skills. We advise the readers to choose a language with which they are familiar.

4.1.2 Time And Relative Dimensions in Space

Animal interactions happen in space, and their distribution on this space determines the pattern and frequency of those interactions (Durrett and Levin 1994). Traditional models of sociality do not explicitly take into account the spatial restrictions, with the notable exception of Hemelrijk and colleagues' extensive work on primate hierarchies (Hemelrijk 1999; Hemelrijk 2002a; Hemelrijk 2002b; Hemelrijk 2004; Hemelrijk 2002c; Puga-Gonzalez, Butovskaya, et al. 2014), and thus leave out a vital component of group formation. Even the Resource Dispersion Hypothesis (see section 2.1.2), which deals with the importance of shared patches of space, has no explicit spatial component in its formulation. More recently, works using game theory like those of Nowak and associates (Nowak, Bonhoeffer, and May 1994; Nowak and May 1992; Ohtsuki, Hauert, et al. 2006; Pacheco, Traulsen, and Nowak 2006) show that the topology¹ of the interactions deeply affects the outcome of those interactions, for instance, causing cooperation to be maintained or lost.

Specially in animals, not only space, but also movement is important, which means that the topology of interactions is constantly changing. Because our questions are related to the spatial distribution of the agents and our interaction definitions are movement-based, our model has to be spatially explicit and our agents mobile. Our space is a continuous surface instead of being discretized into a grid to allow a more precise measurement of distance, but for some models, such as landscape ecology, a discrete space, divided in patches, may be more suitable.

Simulating space and movement

In the model, space is represented as the surface of a continuous, homogeneous torus (see Fig. 4.1). This particular shape allows us to use a Cartesian coordinate system and to avoid boundary problems: agents can move freely through the whole surface, and all distances can be calculated using Euclidean geometry. Another possible geometry for spatially explicit ABMs would be a bounded plane, but the modeller would have to be careful to decide how the agents behave when

¹**Topology:** the arrangement of the nodes in a network. This can be interpreted as their positions in space if edges represent proximity.

Figure 4.1: **The shape of the world.** A shows the agents on a Cartesian plan. B Shows the Cartesian plan wrapped on a torus, thus emulating a world without boundaries. The curvature of the surface of the torus can be disregarded and distances between agents can be calculated using Euclidean distances, avoiding the difficulties of calculating coordinates and distances on the surface of a sphere.

they reach space limits, and pay attention to how this behavior affects model results. World size is also important, as it determines the minimum possible density of agents, which is relevant for our questions about cluster formation: if the agents have nowhere to move to escape agonistic interactions, they will be forced to stay in the same cluster, possibly masking the effects we want to see.

In our model, each individual agent moves one step per turn on a random direction, to a distance of up to 1 step size (defined arbitrarily), if there are no other agents on its neighborhood. We chose this non-correlated random walk so as not to impose any kind of directional bias on the agents. therefore, agents remain randomly distributed throughout the simulation in absence of the effects of social interaction. If there are other agents in the actor's neighborhood, there is the possibility of social interaction (Fig 4.2). Social interaction results in directed movement, as per our definitions in Chapter 2, box 2.2: the actor either moves closer to, or away from, the co-actor, to a distance of up to 1 step size. After repeated interactions, this can result in agent distribution going from random to clustered (Fig. 4.3).

Simulating time

Time scale and whether time is continuous or discrete can have drastic impact on model results. Time scale indicates the amount of time covered between each timestep. Each timestep can mean a second of real time, or can be a more abstract measure such as a generation, depending on the requirements of each model. It is also possible to have more than one timescale if the model

Figure 4.2: **How agents perceive the world.** Shows how an agent (A) chooses to approach or avoid co-actors. A only perceives what is inside its neighborhood radius, represented by the red halo around it. Its memories of B and C are represented list besides each. Blurred agents are beyond the perception radius and therefore cannot interact with A

calls for it, for instance, each agent can have an internal timescale representing internal processes such as decisions or metabolism, and a longer timescale representing population and community processes like extinctions and speciation.

Time in computer models is, due to computer limitations, discrete, but since we are aiming for a relative degree of realism in our model, our agents must act in continuous time, one after the other, based on their surroundings at the time of the action, and not all at once ignoring each other's actions. This means that interactions must happen sequentially, and each agent must have access to the results of previous actions. To do this we use an *asynchronous* interaction scheme (Caron-Lormier et al. 2008), which simulates sequential actions in continuous time.

To illustrate this, suppose we have 3 agents, Charmander, Squirtle and Bulbasaur. Charmander and Bulbasaur are in each other's neighborhood, and Squirtle is closer to Bulbasaur than to Charmander, but out of reach. Suppose the order of actions on this turn is Charmander, Bulbasaur and Squirtle. In a *synchronous* situation, all three act at the same time, according to

Figure 4.3: **Clustered agents vs random agents.** In A we have the initial random distribution of 20 agents. In B, after 15 rounds, individuals are clustered.

the state of the world at the beginning of the current round. This means that Charmander and Bulbasaur will interact, an agonistic interaction, for instance. This causes them to separate and Bulbasaur moves to within Squirtle’s neighborhood, but the result of this interaction will have no bearing on Squirtle’s action until next round, and Squirtle ends up not interacting with anyone on this round.

In an asynchronous situation, Charmander has an agonistic interaction with Bulbasaur, and as a result they move apart. This puts Bulbasaur in Squirtle’s neighborhood. It is then Bulbasaur’s turn, and it now interacts with Squirtle, having an affiliative interaction. This makes them move closer. It is now Squirtle’s turn, and it once again has an affiliative interaction with Bulbasaur.

As we can see, the synchronicity of the actions can have massive impact on the resulting interactions. The asynchronous situation is a better fit for our purposes, given that we are trying to model animals which react to a constantly changing world.

4.1.3 Simulating memory and forgetfulness

The main characteristic our agents have is their memory. Each characteristic of the agents in an ABM must be well-defined, and it’s consequences well studied to understand its implication on model results, as they are part of the model’s premises.

Our agent’s memory is represented as a list of previous interaction, with their respective types, in chronological order. The agent has one separate list for each other agent it has interacted with. To increase the realism of the model, and also to save computational resources, memory has a fixed length. Once this length is reached, the oldest interactions are forgotten and replaced with

new ones. We base this on experimental evidence that individuals forget others after some time (see for instance Briefer, Padilla de la Torre, and McElligott (2012); Bruck (2013); Karavanich and Atema (1998); Sheehan and Tibbetts (2008) and your own personal experience), and this length is highly variable between species. This means that even though memory acts as a positive feedback loop, because our interactions have a random component to it, a pair of agents can pass from being highly affiliative toward each other to being neutral or even agonistic after some time.

Simulating interaction and social preference

The choice of with whom to interact is also important. Even though in our model memory has a positive feedback effect on future interactions, if repeated pairings are not frequent that feedback has little chance to show its effect. Thus, the effects of memory and recognition can be masked just because individuals do not interact enough times with the same other individual. This can actually reflect a natural situation: Sheehan and Bergman (2016) argue that in sufficiently large groups, we do not expect IR to be advantageous, due to the economics of high cost of remembering many individuals versus the low probability of re-encounters.

To investigate whether memory alone has an effect on group formation we explored two different possibilities: *random choice of partner*, and *preferential partner selection*. In the random choice case, the actor chooses one co-actor from the neighbors inside its interaction radius at random. In the preferential interaction method, the actor chooses to interact with the neighbor with whom it has the highest affiliative memory. In a tie, a co-actor is chosen at random from the highest affiliative ones. In both cases, the type of interaction is dependent on memory. We found that, in our model, memory alone had a very small effect on group formation unless this memory also resulted in preferential interaction. The random choice of partner results were essentially the same as no memory. This shows that even though memory may exist on a system, its signal can be drowned in the noise of random interactions, if the amount of noise is sufficiently large. Preferential interaction increases the effect of affiliative memory, increasing group formation and changing its structure. In the next chapter we will explore in more depth the preferential interaction case.

4.2 Output and analyses

It is not sufficient to build and run the model, we must be able to analyze its results to draw meaningful conclusions, thus special care must be given to how the model outputs its results. We follow the "virtual ecologist" approach of Zurell et al. (2010): data should be collected from simulations as it would be from real experiments. This allows model data to be compared to field or experimental data when possible, and also serves to guide model building: by keeping in mind what would happen if we were doing a real experiment, we maintain a degree of realism and avoid excessively abstract, non-mechanistic models. This is specially important in our case, as we are essentially testing the consequences of a mechanism of group formation.

Our model outputs several text files containing, for each timestep, the number and composition of spatial clusters, and at the end of the simulation run, a file containing the final social network of the agents. This allows us to use standard techniques of cluster analyses and social network analyses, in a way that is comparable to field data.

An important output which is often overlooked is the visual output of the simulation. Humans are visually oriented animals, and even when using your programming language's debugging features, it is important to see your agents on the screen, specially when first writing the code. Problems with movement algorithms, distance calculations, interactions, world boundaries, and others are quite difficult to catch only by looking at numbers changing on the screen, but are easily spotted when looking at moving agents. Some languages are visual by design, like NetLogo, but almost all languages have features that can be used to build a crude interface or visual output (We used the Qt framework for this purpose). Once the code is finished and debugged, the visual interface can be turned off to speed up processing.

We end this chapter echoing the advice of Grimm and Railsback (2005): keep your model as simple as you can. As more things are added to a model, it becomes more difficult to analyze and debug, and more hidden premises are added. Add only the characteristics necessary to study what you want, no less and no more than that. We also advise to build the model in increments, to make it easier to find errors. In our model, first we coded the world, then the agents. After that we added movement rules, and finally we added memory and preferential interaction, testing all the way. Though this step-by-step approach this takes much longer than coding the whole model at once, and though our code is certainly still not perfect, we were able to detect many coding

mistakes this way, and had we not done so we would not have found that preferential interaction is a requirement for individual recognition to show the effects we see in the next chapter.

5 — Do I know you?

How individual recognition affects group formation and structure

Abstract

Groups in nature can be formed by interactions between individuals, or by external pressures like predation. It is reasonable to assume that groups formed by internal and external conditions have different dynamics and structures. We propose a computational model to investigate the effects of individual recognition on the formation and structure of animal groups. Our model is composed of agents that can recognize each other and remember previous interactions, without any external pressures, in order to isolate the effects of individual recognition. We show that individual recognition affects the number and size of groups, and the modularity of the social networks. This model can be used as a null model to investigate the effects of external factors on group formation and persistence.

5.1 Introduction

5.1.1 Group living

Animal aggregations have long interested researchers. The idea of several animals living in close proximity seem, at first glance, counter intuitive: proximity can bring with it a host of disadvantages (Alexander 1974): increased chance of pathogens transmission, increased visibility to predators, increased demand for scarce resources, increased chance of intraspecific competition, and even reduced direct fitness (Sherman et al. 1995), for instance. However, under some circumstances, aggregations can be beneficial for an individual, if not for the whole group. For instance, there can be safety in numbers: even though a large group is more visible than a single individual is, the probability of any single individual being predated is decreased when there are many others from which to choose (Hamilton 1971). Group living also allows for individuals to share resources when these are scarce or unevenly distributed, and for better vigilance against predators or competitors (Clark and Mangel 1986). Group living can also lead to more cost-efficient burrowing (Ebensperger and Cofré 2001). Large aggregations of animals can happen without visible direct interactions other than mere proximity (Hamilton 1971), and these aggregations can display quite intricate collective behavior, even in the absence of perceived communication (Hildenbrandt, Carere, and Hemelrijk 2010). Groups can also be highly compact and highly interactive, as in colonies of social rodents, where the individuals share resources and interact frequently (Lacey and Wiczorek 2003). These groups can be quite large, or comprise only a breeding pair and its offspring. There are also fission-fusion societies, in which social bonds can last for a long time, that is, repeated interactions are frequent between individuals, but in which spatial relationships are often not constant, with individuals frequently separating (fission) only to regroup later (fusion) (*e.g.*, bats, Kerth, Perony, and Schweitzer 2011).

Current models of sociality rarely take movement or space into account (see for instance (Johnson, Kays, et al. 2002; Johnstone 2000)), but animal interactions happen in space, and, barring a few sessile groups, animals are motile. These characteristics shape the interactions and their consequences: animals can leave groups to forage and return, or can be forced to leave permanently due to agonistic interactions. Groups can also defend home ranges and share resources, and it has been shown that space is an important factor in the evolution of cooperation

(Nowak, Bonhoeffer, and May 1994).

These different kinds of groups give rise to several questions: if groups can be induced externally (*e.g.*, by predator pressure) or internally (*e.g.*, by generation overlap), how, if at all, do repeated individual interactions alter the group's structure? Do preferential interactions lead to different group dynamics? Do groups based on repeated interactions last longer than groups formed by external pressures?

For repeated interactions between a pair of individuals to have an effect different from a series of random encounters, it is necessary that the pair in question react to each other differently than they would react to a stranger. In other words, memory, in the form of recognition, must exist. Recognition can be as specific as *individual recognition (IR)*, in which an individual associates a particular conspecific with some specific information (Tibbetts and Dale 2007), or as general as *class-level recognition*, where the information is associated with a certain trait that can be shared by many conspecifics, *e.g.*, a colony odor, as in honeybees (Breed 1998).

We seek to investigate how do memory and individual recognition affect group structure and stability, by using a computer simulation approach. Using a spatially explicit model, we can investigate the effects of individual recognition in repeated interactions with movement in space, which will help us answer our questions. We expect that simulations with individual recognition will give rise to groups with different characteristics and durations than simulations without it.

5.2 Methods

In this paper, we define *group* as “a spatial aggregation of conspecifics”, regardless of presence or absence interactions between the individuals it comprises. We choose to use a purely spatial definition as we intend to study the effects interaction have on grouping, and including interaction directly on the definition would be troublesome for this purpose. We purposefully avoid using terms like *society*, *colony*, *band*, *flock* and others as they are loaded with meaning, and can imply a defined group structure. *Group structure* here refers to “the pattern of social behaviors between individuals in the group” and *group stability* is “group persistence trough time”.

5.2.1 How to investigate memory?

Agent-based models (ABMs), also known as individual-based models (Grimm and Railsback 2005), are a computational tool that allows us to model the traits and behaviors of individuals,

which can differ between individuals. Each agent in the model can have its own behaviors and internal state and history, and this history can alter how the agent behaves. These characteristics make ABMs ideal for modelling memory, as memory is nothing more than an individual's particular history. ABMs also allow for perfect control of the virtual experiments, eliminating possible sources of confusion, such as resource distribution and competition from other species. By running simulations identical except for presence or absence of memory, we are able to isolate any possible effects memory has. ABMs can easily model the effects of space and movement on social interaction (Hemelrijk 2000b). Here we use an ABM to model individual interactions and to monitor group formation and changes on group structure in a homogeneous space, without external confounding factors.

5.2.2 The model

We refer the reader to section 5.7 - ODD Protocol for the model's full description and ODD protocol (Grimm, Berger, et al. 2010). Here we give a brief explanation of how our model works. The full code of the model is available at <https://github.com/vrios/SocS>. The individuals, called *agents*, exist in a world without physical obstacles or constraints other than world size. The general model is summarized in Fig. 5.1. Each agent moves freely in a random walk, until it encounters another agent. The result of this encounter is a behavior that depends on the agents' memory: they have a higher probability of repeating previous behaviors than of engaging in different ones. In other words, if they have had more affiliative encounters than agonistic ones, they probably will have another affiliative encounter, and vice-versa. If the agents have not encountered each other previously, one behavior (agonistic, affiliative or neutral) is chosen randomly, with equal probabilities for each kind. The behaviors are represented by movement in the model: in an affiliative encounter, the acting agent moves closer to the other one, while in an agonistic encounter, it moves away. In a neutral encounter, the agent moves randomly.

These three types of behavior were chosen to represent the three possibilities animal have when meeting a conspecific: to act affiliatively (cooperating or allogrooming, for instance), to act agonistically (territorial displays or fights), or to ignore each other. We vary the magnitude of the effect memory has by changing the durations of memory from remembering zero encounters to remembering 30 encounters with each other agent, and by varying the intensity of the effect individual recognition has on the behaviors. The probability of engaging in the same type of

Figure 5.1: Simplified fluxogram of the model Panel A shows the order of events in each round. Panel B shows the encounter procedure.

behavior increases by a given amount with each interaction, and this amount ranges from 0.5% to 50% per interaction.

5.3 Analysis

We analyze the resulting groups from two different perspectives, spatial and social. Since our definition of group is spatial, we use a spatial clustering algorithm, DBSCAN (Ester et al. 1996), to investigate whether simulations with IR result in different spatial patterns. DBSCAN gives us the number, size and composition of spatial groups. This allows us to compare whether groups survive in time using the MONIC algorithm (Spiliopoulou et al. 2006), which compares group composition in successive moments. Thus, our spatial metrics are number of groups, average group size, and average group lifespan. We predict that these three metrics will all be larger in simulations with IR.

These metrics tell us about the aggregation, but do not inform us about the how groups formed by, por eample, spatial constraints, differ from those formed by social interactions. It is to be expected that higher densities lead to larger group sizes, but this does not mean that the individuals in those groups interact with each other. To examine the social consequences of IR we use social network analysis (Newman 2003). Social networks can be used to describe interactions between individuals in the form of graphs, with individuals as nodes and interactions as edges, with stronger interactions having higher edge weights. Differences in connectivity and connection strength can give rise to a modular network. Modular networks are networks which are divided in subsets, called modules, in which nodes are more strongly connected to each other than to nodes outside of these subsets (Newman 2006). In our model an edge is formed whenever two agents interact, and the weight depends on the type of interaction: -1 for agonistic, 0 for neutral and +1 for affiliative. The sum of all interactions, positive and negative, between two agents determines the final weight of the edge, and thus describes the prevailing type of interaction between those two agents. Individuals in close proximity will have a higher probability of interacting whith each other than with distant individuals. If the type of interaction is based on previous interactions, we should see a higher modularity than if the interations happen randomly. We calculate modularity using the Louvain algorithm (Blondel et al. 2008), taking into account only the positive weights of the edges at the end of the simulations, that is, the modules are based only on primarily affiliative interactions.

Figure 5.2: **Mean number of clusters without (A) and with (B) memory.** Each colored line represents one replicate, total of 20 replicates. World size = 79 units, 1000 agents, memory in A = 20 timesteps, memory modifier = 5%. This shows the effect of IR on aggregation: more groups are formed when individuals recognize each other than with only random interactions.

Since our models have a strong probabilistic component, all metrics are presented as the average of 20 replicates with the same starting conditions, run for 1000 rounds. Simulations and DBSCAN were written in C++11 using the QT 5.0 framework (<http://www.qt.io/>). Analyses were made in R version 3.2.1 (R Core Team 2015) using the Igraph package (Csárdi and Nepusz 2006), and MONIC version 1.0 (Spiliopoulou et al. 2006). We used parameter values for DBSCAN of $Epsilon = 3$ and $MinPts = 4$, the values recommended in literature for clustering in 2d space (Ester et al. 1996) Simulation and analysis code is available upon request.

5.4 Results

5.4.1 Spatial group size and number

After a short transient period, the number of groups in simulations without IR decreases dramatically (Fig. 5.2, panel A), from about 30 in the beginning to less than 10 at the end, while it increases in simulations with IR (Fig. 5.2, panel B), from about 30 to around 50 in average. The opposite is seen for average group size (Fig. 5.3), in a much more drastic manner: average group size increases dramatically without IR (Fig. 5.3, panel A), to the point where, in some moments, over half of all agents are in the same cluster (cluster sizes of over 600 in some cases). With IR, group size drops slightly relative to starting conditions (Fig. 5.3, panel B), but ending being an order of magnitude smaller than the no-IR case. This means that the repeated interactions not only are making the average number of group larger, they are keeping them physically separate, so that we have many small groups at the end of the simulation. Though we detected a difference

Figure 5.3: **Mean size of clusters without (A) and with (B) memory.** Each colored line represents one replicate, total of 20 replicates. World size = 79 units, 1000 agents, memory in A = 20 timesteps, memory modifier = 5%. Average group size differs dramatically when IR is introduced, remaining relatively constant and low, while it increases and varies dramatically when there is no IR (note the different scales on the y axes). This shows the effect of IR on aggregation: smaller, groups are formed when individuals recognize each other than with only random interactions.

with the presence of IR, memory intensity and duration did not cause significant differences in group number or size (Fig. 5.4). Group duration was similarly higher in simulations with IR than without.

Population density also has an important effect in spatial grouping. When density is too high, the effects of IR are harder to see, due to limitations of the cluster algorithm: the individuals are too close for DBSCAN to detect distinct groups reliably, and most agents end up being part of a giant cluster (see figs. 5.5, 5.6). For a matter of consistency, we use the same DBSCAN parameters for all simulations. While using distinct parameters for different densities would

Figure 5.4: **Effects of shorter memories.** Panels A and B show Mean cluster size and mean number of clusters. Each colored line represents one replicate, total of 10 replicates. World size = 79 units, 1000 agents, memory in A = 2 timesteps, memory modifier = 5%. The same pattern is seen in Figs. 2 and 3 of the manuscript, showing that the mere presence of IR is sufficient to induce group formation.

Figure 5.5: **Effects of high density.** Panels A and B show that at high densities, all individuals are forced into a single cluster most of the time. Each colored line represents one replicate, total of 10 replicates. World size =45 units, 1000 agents, memory in A = 20 timesteps, memory modifier = 5%.

possibly detect more groups, these groups would not be comparable between simulations, as they were detected differently. Though this seems an arbitrary limitation, it can be seen as reflecting a real-world situation: when space is an issue, animals will be forced to live closely together, even if they do not interact much.

5.4.2 Social networks

IR also had an effect on network modularity (Fig. 5.7 and Fig. 5.8). Modularity was slightly lower in simulations without IR than in those with IR, meaning that the groups found were more tightly linked. Here we also observed an effect, though slight, of memory intensity: modularity increased slightly when memory intensity was higher.

Figure 5.6: **Effects of low density.** Panels A and B show that at low densities, no clusters form, as individuals are too spread out. Note that the minimum size for a cluster to be detected with DBSCAN is 4 individuals. Each colored line represents one replicate, total of 10 replicates. World size =250 units, 1000 agents, memory in A = 20 timesteps, memory modifier = 5%.

Figure 5.7: **Social network at the end of one simulation.** Social network at the end of one simulation. Nodes represent agents; each color represents a different module. Edges are shown in grey. Though edge strength was used to calculate modularity, it is not shown in the graph due to the high number of edges. World size = 79 units, 1000 agents, memory length = 30 time steps, memory modifier = 10 %. Nodes in the graph are arranged according to interaction strength: distance between nodes is inversely proportional to the strength of their interactions, i.e., closer nodes have had more affiliative interactions. Distances in the graph are not representative of spatial distances in the simulations.

5.5 Discussion

To approach the question “how do memory and individual recognition affect group structure and stability” we face serious problems: it is difficult to isolate the effects that memory has on social behavior from those caused by other factors, such as resource availability, age and

Figure 5.8: **Modularity values without (A) and with (B) IR.** Modularity values without (red) and with (black) IR. $N = 20$ replicates for each. World size = 79 units, 1000 agents, memory in A = 20. Values in red differ significantly from each other and from black ones, $p < 0.01$, Kruskal-Wallis test and Dunn’s multiple comparison test. Black values do not differ significantly from each other.

reproductive state. It can also be extremely difficult to determine whether a species exhibits individual recognition or is merely able to determine whether a conspecific falls into a general class (see Gherardi, Aquiloni, and Tricarico (2012) for a treatment of this problem). Further, if we were to examine the effects of IR, it would be tremendously useful to be able to turn it off and on, to compare the effects of its presence with those of its absence. Though there are methods to experimentally alter the levels of affiliation individuals from a given species exhibit (Young et al. 1999), there is currently no way to do this with individual recognition, and doing so could raise ethical questions about the use of transgenic animals. Thus, we use computational modelling to investigate memory and individual recognition, instead of using traditional experiments with live animals.

These simulations indicate that IR does indeed affect the structure of groups. The preferential interactions between individuals result in higher modularity than in simulations without IR, and groups are more spatially discrete. Thus, even though external pressures, which can result in increased densities, can lead to increased grouping, groups created by social behaviors have intrinsically different social structures.

Our results also show that when IR is coupled with preferential interaction, it can result in smaller group sizes than when there is no recognition. Sheehan and Bergman (2016) discuss that social recognition (and, by extension IR) should only be advantageous in small groups, as the formation and retention of individual memories quickly becomes too costly, and therefore IR should be under negative selection in large groups, being superseded in fitness gains by quality signalling. Indeed, in some of the largest known groups, such as honeybee hives and fish swarms, there is no evidence of individual recognition. We show here that the presence of IR can be a driver for small group sizes without invoking any costs whatsoever, as our model includes no form of fitness payoff or energy expenditure. This is due to the fact that in our model IR results in a positive feedback loop of agonistic and affiliative behaviors: agents who have had an agonistic encounter will tend to remain separate, helping to define spatial groups.

Studying IR can help answer several questions about sociality and animal interactions, for instance, how animals decide whether or not to aggregate or share resources when confronted with resource depletion. Recognition of familiar individuals could increase the probability of repeated interactions, giving rise to forward-feedback phenomena such as reciprocal altruism, and to colony formation. Another more practical application of IR and social memory studies

would be in conservation of endangered animals. Fauna translocations are often used to mitigate ecological impacts, but if this is done without consideration for the social systems of the affected species, it can do more harm than good. Introducing foreign individuals to established groups can cause the introduced individuals to be rejected or killed, reducing the success of the translocation, as would separating individuals from their established groups. Knowing whether a species aggregates because of space or resource constraints, or due to social interactions would help plan the translocation or reintroduction of individuals to minimize harm.

This work does not take into account factors like resources, reproduction or fitness, thus providing a null model of the effects of individual recognition in a fixed population. We believe that this type of model can be a powerful resource to compare with other models and experiments. Simulations allow us to investigate aspects of our systems that would otherwise be hard to approach experimentally, and the ability to isolate and manipulate the mechanisms and processes of interest is especially useful. Null models such as this can serve to generate null hypotheses which could be used to design traditional experiments and field investigations, as King et al. (2011) have done. The use of agents and movement to create an interaction network is a novel and promising approach in animal behavior studies, and allows for a wide range of scenarios to be investigated.

Here, our simulations were identical, except for the presence or absence of IR. If we were to do a traditional experiment to try and answer our questions, we would either have to resort to using closely related, but ultimately different, species, or to come up with a way to “turn off” individual recognition in our test subjects. Either approach would bring about problems and confounding variables. Turning off IR would mean blocking memory formation, retention, and/or recollection, either chemically or via genetic modification, but this could affect other important social behaviors or other types of memory. Infusion of oxytocin, for instance, has been shown to increase duration of social memories Dluzen et al. 2000, but oxytocin and its non-mammalian analogues also affect other social and non-social behaviors Donaldson and Young 2008; Gruber 2014, which would affect group structure in unknown and possibly uncontrollable ways. Using related species is ideal for studying how IR evolved from a non-IR situation, as Sheehan, Straub, and Tibbetts (2014) have done with Polistine wasps, but even closely related species can have highly different social patterns, as chimpanzees and bonobos (Palagi 2006), which would complicate analysis. Thus, this comparative approach could be unsuitable for

many species. Using the example of faunal translocation above, it would be relatively simple to modify the simulations to have the agents moving on a GIS map, and after the groups are established, to add new individuals into the simulation to see whether the groups remain stable or if the introduced individuals are rejected. Fine-tuning of the simulation parameters to match the species of interest would not be difficult, since it would be mostly adjusting the action probabilities to match a more social, solitary or aggressive species, and creating pre-established groups, by creating agents with pre-built memory histories. This simulation framework could also be modified to investigate the evolution of social traits. Here IR is a binary phenomenon, it either exists or not, but a more complex approach could be made by breaking IR into its basic components, (phenotypical variation of identity cues, perception of these cues, and the action taken based on this perception, see Mateo 2004), and making these components variable and inheritable in the simulation. Another approach would be to investigate if class-level recognition leads to different group structures than individual recognition, or if IR and class-level recognition are functionally the same after a certain group size

5.6 Acknowledgments

The authors would like to thank Prof. Paulo Inácio Prado from the University of São Paulo, for the use of computational resources for the simulations

5.7 ODD Protocol

This is the OOD protocol describing our model, as proposed by (Grimm, Berger, et al. 2010). It is intended as a verbal description of the model to allow understanding and re-implementation of the code if necessary. The full source code for our model is available upon request.

If we are to study sociality and group behavior, it is important to clarify exactly what we mean by “social behavior”, “group”, “memory” and other terms, so that we can properly analyze and model them, especially because this field of study is fraught with multiple, conflicting definitions (see (Costa and Fitzgerald 2005), for an analysis of this problem).

Social behaviors are defined here rather loosely as “any interaction between two conspecifics”. Though this definition is certainly not a consensus, it is useful and sufficient for our purposes, as it avoids biases towards “socio-positive” behaviors such as allogrooming and mating, and includes aggressive behaviors, which are usually not seen as “social”, but affect a group’s structure and

stability. We divide social behaviors in two categories, based on their long-term effects on the group: *affiliative behaviors* are “behaviors which tend to increase grouping” and *agonistic behaviors* are “behaviors which tend decrease grouping”. Thus, mating and food sharing are affiliative behaviors, in that the proximity they cause is long lasting. A fight is considered an agonistic behavior because, while it certainly brings individuals together for the duration of the event, it is safe to say that at least one of the animals will leave the area afterwards, especially in territorial disputes (unless one of the animals perishes). *Interactions* and social behaviors are used interchangeably here. These definitions are based purely on movement, to reflect our definition of group. All behaviors that do not involve interaction with other conspecifics directly, that is, which do not affect the group, are lumped together as *neutral behaviors*. Neutral behaviors can bring individuals closer or apart, but this proximity is not derived from interaction, and therefore not social under our definitions. As our definition of group is not based on social interactions, neutral behaviors can give rise to groups, but it is expected that these groups will be short-lived, as the non-interacting individuals go about their businesses. These definitions may appear to be oversimplifications of complex phenomena, and it would certainly be more realistic to add gradations to the intensity of each type of behavior, but doing so would add unnecessarily complexity to the model. A simple affiliative/agonistic/neutral classification of behaviors allows us to compare situations with and without memory without worrying about the effects of affiliation or aggression levels, or the external causes of these behaviors.

Since we are interested on the effects of repeated interactions, definitions of memory and individual recognition as they pertain to social behaviors are also required. Here, *memory* is defined as “an individual’s record of its previous interactions (*social behaviors*) with other conspecifics” and *individual recognition* (IR) is “the ability to associate a particular memory with a particular conspecific”. We will use the terms *memory* and *social memory* interchangeably. Though other types of memory are important for the individual’s survival, we will not concern ourselves with them here. The mechanisms by which individuals recognize each other and by which memories are formed are not relevant for this paper. We will use these basic definitions to create a model of social memory to investigate its effects on group formation and structure. Simulating perfect memory, that is, remembering all previous encounters with all other agents would be computationally prohibitive due to the size and length of the simulations.

1. Purpose

What is the purpose of the model?

This model intends to explore the effects of memory and individual recognition on group formation and structure. In other words, we review how the effect of past interactions affect the structure and stability of groups in a population of agents.

2. Entities, state variables, and scales

What kinds of entities are in the model? By what state variables, or attributes, are these entities characterized? What are the temporal and spatial resolutions and extents of the model?

The only two entities present are the world and the agents. The world exists as a proxy for space, and its only actions are to define the order of interactions, and to keep a register of the agents' spatial coordinates. In all simulations the world is represented by the surface of a torus, that is, a 2d space with continuous boundaries, homogeneous, and without corners. The size of the world varies between to simulate different agent densities.

Each agent is a separate individual, representing a freely moving animal with independent behaviors. The agents are points in space, and have only 6 important traits: *position*, *perception radius*, *step size*, *action probabilities*, and *memory*.

- (a) *Position* is the agents X and Y coordinates
- (b) *Perception radius* is how far in space the agents can perceive one another.
- (c) *Maximum step size* is the maximum distance an agent can move in a single action. A single step is a random length between 0 and *maximum step size*.
- (d) *Action Probability* describe how likely an agent is to engage in one of three behaviors when in a social situation: affiliative, agonistic and neutral.
- (e) *Memory* is a record of the previous interactions each agent has had with other agents, and described by *memory length*, the maximum number of interaction an agent can remember, and *memory intensity*, how strongly each remembered interaction affects the agents' action probabilities (see below). All agents are initially identical, differing only in their initial coordinates, and all have empty initial memories
- (f) *Space* is measured in arbitrary units, as time is measured in rounds. All agents act only once per round. Each action is a step and a possible interaction with a single other agent. See below for details of interactions

3. Process overview and scheduling

Who (i.e., what entity) does what, and in what order? When are state variables updated?
How is time modeled, as discrete steps or as a continuum over which both continuous processes and discrete events can occur?

On each round, each agent is called to act and possibly interact with the surrounding agents. The calling order is randomized at the beginning of each round, and all agents are called once per round. Each agent has access to the current state of the world around it, with the updated positions after the previous agent has acted. This asynchronous updating simulates a continuous time process (Caron-Lormier et al. 2008). Each round occurs as follows:

- (a) Round starts, World randomizes order of agents
- (b) Each agent (called *actor* when on its turn to act) performs the following procedures once. All agents act, one after the other, in the order determined in step 1
 - i. Actor searches perception radius for other agents
 - A. If there are any, choose the one with whom actor has the highest affiliative memory and proceed to the *encounter* sub-process, and both agents' memories are updated accordingly
 - B. If no other agents in perception radius, actor takes a step of random length (from 0 up to *step size*) in a random direction
 - ii. Actor position is updated on the world
- (c) Round ends, statistics are collected, proceed to next round.

As actor positions are updated constantly, each agent has access to the current state of the world. This approximates a continuous time, even though round are discrete and non-overlapping.

If actor finds at least one other agent in its *perception radius*, it chooses the one with whom it has the highest count of affiliative events in its memory. If more than one has the same count, one is picked at random. This is intended to mimick the phenomenon where affiliative memory induces preferential interactions, that is, given a choice, all things being equal, animals will prefer to interact with familiar animals. Test simulations have shown that when the actor chooses a partner at random, the effects of recognition are diminished.

The *encounter* sub-process is described in Submodels, below.

4. Design Concepts

(a) Basic Principles

The most basic principle in this model is that memory has an effect on an individual's decision on how to behave relative to familiar individuals. (See main paper for reasoning behind these behaviors)

When confronted with another individual, an actor has three options: it can ignore the other, a behavior we call *neutral*; it can engage in an *agonistic behavior*, e.g. an aggressive display or a fight, or it can engage in *affiliative behaviors*, such as grooming or sharing resources. We assume that each of these social behaviors has a different consequence on group formation and maintenance: *Neutral* behaviors do nothing at all for the group. The actor proceeds as if there had not been an encounter. *Affiliative* behaviors increase group cohesion, that is, the actor steps closer to the other agent. *Agonistic* behaviors are the opposite, that is, the actor steps away from the other agent

(b) Emergence The group or groups emerge from the interactions of individuals agents.

A group is determined spatially as a cluster of individuals using the definitions of clusters from the DBSCAN algorithm: groups of points, which are density-connected, that is, are within a certain distance from at least one other member of the cluster. See the DBScan algorithm section for details.

Spatial clusters are calculated at the end of every round. After the simulations ends, the clusters from each round are compared using the MONIC algorithm

(c) Adaptation

Agents react to the presence of other agents based on the memory of previous interactions. They can ignore, approach, or avoid other agents, depending on their memory, with a cumulative effect

(d) Objectives

Agents do not have an explicit objective. They move randomly until they meet another agent. Even when meeting another agent, they act based on an action probability, not an explicit intention

(e) Learning

Individuals learn what type of interaction they had, and the identity of the agents with whom they interacted. Memory also has a definite length, after which older

interactions no longer affect the outcome of the current interaction

(f) Prediction

Agents are not capable of prediction

(g) Sensing

Agents can sense the presence of another if they are within their perception radius. They can perceive the others' identities and remember previous interactions. They always choose to interact with the individual with whom they had more affiliative interactions.

(h) Interaction

The agents can approach, avoid or ignore each other. If they have an affiliative interaction, the actor approaches the target agent. In case of an agonistic interaction, the agent moves away from the target agent, and if the action is neutral, the agents moves randomly. The type of interaction is chosen based on the actor's action probabilities, modified by its memory

Each actor can only interact with one other agent on each round

(i) Stochasticity

The interactions are based on action probabilities. Each agent has an initial probability of 1/3 for each action, affiliative, agonistic or neutral. This means that if there is no effect from memory (if the agents have never met) the type of interaction is random, with equal probabilities. These probabilities are modified according to the memory submodel below, but are always between zero and one (not inclusive), that is, even if the agents have always acted affiliatively, there is a small chance they can act agonistically or neutrally.

(j) Collectives

There are no explicit collectives. Clusters are calculated at every step, but have no bearing on an individual's action. The individual has no concept clusters or grouping.

(k) Observation

At the end of each round, spatial clusters are computed via DBSCAN, and a register is kept of who interacted with whom and how (what type of action was performed). At the end of the simulation, the MONIC algorithm is run to calculate lifetime of the clusters. The sum of the actions between two agents is also calculated (affilitives

are counted as +1, agonistics as -1 and neutrals as 0), and this is used to investigate the social networks formed between the agents. The number of clusters and average cluster size is also registered for each round

5. Initialization

At time $t=0$, the agents are distributed randomly throughout the world. All agents are identical and all memories are empty. There are 1000 agents, but the world size varies to simulate different densities. Interaction radius is 3 units, step size is 2 units. Epsilon and MinPts (see DBSCAN below) are 3 and 4, respectively. These values were taken from (Ester et al. 1996), which describes these values as being adequate for two-dimensional spaces. Memory length and effect size are also set at initialization, but vary between simulations

6. Input data

There is no external input data other than the parameters described above

7. Submodels

(a) Action

Actions are modeled as movement. Since we define a group as an aggregation of individual which persists in time, affiliative actions are defined as those that aggregate individuals, and agonistic action are define as those which tend to segregate individual. Neutral actions are defined as not having a direct impact on grouping and therefore are represented by random motion. If there no other agents on an actor's perception radius, then it moves in random direction, to a distance of up to its maximum step size.

After an affiliative encounter, the actor takes a step in the direction of the target agent. Because step size is random (between 0 and *stepsize*), and can be slightly greater than the distance between the agents, they do not converge on a single spot a sequence of affiliative interactions. After an agonistic encounter, the actor takes a step in the opposite direction

(b) Memory

The agent's memory is composed of a list of interactions with a given *memory length*. This length is fixed at the start of the simulation. Each agent has a different list for each agent whit whom it has interacted. Interactions are added to this list, and once

the maximum length is reached, the oldest interaction is removed to make space for the newest one. The three types of action are added to the same list. This implies that an individual's memory towards another can change with a sequence of interactions. Memories also have an *intensity*, that is, the amount that is added to the agent's initial action probability to determine the outcome of the encounter. This intensity is assumed constant and equal for all interaction types. The three action probabilities that must always add up to one, and can never be zero (the minimum value for each is 0.05%, and the maximum 99,9%).

(c) Encounter

The encounters are determined in the following way: the actor scans its memory for previous interactions with each other agent in its interaction radius, and chooses the one with whom it has the highest affiliative modifier. Action modifiers are calculated according to the following formulae:

$$\text{Affiliative modifier}(af) = \text{total Affiliative actions} * \text{intensity modifier}$$

$$\text{Agonistic modifier}(ag) = \text{total Agonistic actions} * \text{intensity modifier}$$

$$\text{Neutral modifier}(an) = \text{total Neutral actions} * \text{intensity modifier}$$

Once the target agent is chosen, the action probabilities are calculated as follows:

$$\text{Affiliative} = \frac{1}{3} + af - \frac{ag}{2} - \frac{an}{2} \quad (5.1)$$

$$\text{Affiliative} = \frac{1}{3} + ag - \frac{af}{2} - \frac{an}{2} \quad (5.2)$$

$$\text{Affiliative} = \frac{1}{3} + an - \frac{af}{2} - \frac{ag}{2} \quad (5.3)$$

To calculate the affiliative probability, we add the affiliative modifier to the base action probability and subtract half the agonistic modifier and half the neutral modifier. This is because these probabilities are complimentary: increasing one must forcefully decrease the other two in equal measure, and they must always add up to one. The same is done for the other probabilities: the final value is the sum of its modifier, minus half of each of the modifiers of the other actions. These probabilities are never allowed to exceed 99,9% or to go below 0.05%. This is to reflect the fact that even though two animals can have extremely high affiliation levels, there is still

the possibility of agonistic or neutral events, and the same holds true for levels of agonism and neutrality.

The type of action to be performed is then drawn from these probabilities by using an uniform distribution random number generator. Once the type of action is determined, the actor acts as follows: if the action is affiliative, the actor and the target move toward each other. If it is agonistic, both move away from each other. If the action is neutral, the actor moves in a random direction. Both the actor and the target then register the interaction in their memories.

- (d) The positions of all agents are fed into the analyses algorithms (see below)

5.7.1 Analysis Algorithms

DBSCAN

Though not part of the simulation *per se*, *DBSCAN* (Ester et al. 1996) and *MONIC* (Spiliopoulou et al. 2006) are an important part of the model results' analyses and are therefore included here. *DBSCAN* is a clustering algorithm that happens to be a close match to the group definition we use in this paper: clusters are defined by a minimum density and can be any shape or size beyond a certain minimum, and points can also be noise, that is not belong to any cluster. It is dependent on two parameters: *Epsilon*, the neighborhood radius of a point; and *MinPts*, the minimum number of points that have to be inside a given point's *Epsilon* for the set (center point plus neighbors) to be considered a cluster. In this paper, each agent is assumed to be a point for clustering purposes.

This procedure returns a set of clusters with its member points, and the points that are not members of any cluster (noise). The results of this clustering for each point in time are the processed by the *MONIC* algorithm to investigate the duration of the groups. The algorithm is as follows:

1. For each point:
 - (a) Check neighborhood in range *Epsilon*.
 - (b) If there are less neighbors than *MinPts*, point is considered noise.
 - (c) If there are more neighbors than *MinPts*, a cluster is found Each point found in this cluster is marked as part of the cluster, and its *Epsilon* neighborhood is searched, and any neighbors found are also marked as part of the cluster. This is repeated for all

points found inside all *Epsilon* neighborhoods, until no more new points are found in the *Epsilon* neighborhood of any member of the cluster.

- (d) Proceed to next unmarked point.

MONIC

MONIC compares sequential clusterings and finds which clusters have survived in consecutive timesteps, by comparing which sequential groups are composed of at least 50% of the same individuals. Doing this this for all rounds allows us to calculate the average lifetime of groups

6 — Closing Remarks

In this thesis, we aimed to provide a broader view of animal sociality, its external and internal drivers, and how to approach it from a modelling perspective. Here we summarize the highlights of each chapter and what we have learned from it.

In **Chapter 2 - Sociality**, we reviewed how groups can be positively selected via fitness benefits, both direct and inclusive. We looked at current models of sociality and how they explain group living. We review the three main mechanisms for group formation from literature, and the limitations of each.

The *Resource Dispersion Hypothesis* model proposes a mechanism in which, given a clustered distribution of food inside a territory, all that is necessary for groups to form is for territory holders (primaries) to tolerate the presence of conspecifics (secondaries). This tolerance of the primaries, coupled with food availability, is incentive enough for other animals to join the territory. If the secondaries are related to the primaries, for instance offspring which have delayed dispersion, then it is easy to see how the inclusive fitness accrued from tolerating their presence can benefit the primaries, even if the secondaries do not contribute to territory defense. This model is interesting because it provides a basis for different, more elaborated forms of sociality to evolve, as it provides a mechanism for aggregation based only on tolerance of conspecific presence. Once animals tolerate the presence of others, more complicated interactions can take place.

The *Selfish Herd* model shows that groups can be formed even in the absence of resource

pressures, and also without interaction, due only to self-preservation instincts. The dilution of individual risk caused by joining a group can give rise to extremely large groups, which can also open the door to other types of sociality.

The *Reproductive Skew* family of models is a framework that explains why individuals can give up their own reproduction in favor of others, most notably even in the absence of relatedness.

In **Chapter 3 - Recognition And Sociality**, we presented our argument for the importance of studying Individual Recognition, and quickly reviewed its neurological basis and modelling strategies.

In **Chapter 4 - Model building**, intended as a primer on agent-based modelling, we guided the reader through our modelling decision process, detailing the decision and their consequences on the models results. We showed an unexpected insight gained from a bottom-up modelling process, namely the importance of preferential interactions, which would have been missed if we had built the model completely at once. We hope to have shown here that the decisions taken while building the model are as important as its premises in terms of consequences on its results.

In **Chapter 5 - Do I know you?**, we introduced a model which can be used to investigate the consequences a particular driver of aggregation, individual recognition. We show that groups formed by individual recognition are different from groups formed by random chance, both in terms of group size and number, and in terms of intra-group social networks. Our model also agrees with the predictions of Sheehan and Bergman (2016) regarding group size, namely that individuals recognition can result in smaller group sizes. We have shown that groups can be formed in the absence of fitness rewards or external incentives such as territory resources or predation pressures, which are the three factors most commonly seen as drivers of sociality.

We end this thesis by noting that our model can be expanded to include other factors. Though we did not include fitness costs in the model, an obvious and realistic addition would be to include a cost for memory storage, which could show when IR is favored over CLR. Given that memory is a costly neurological process, one should expect individual recognition to exist only when it provides a significant fitness advantage over class-level recognition or lack of recognition. As Sheehan and Bergman (2016) point out, once the number of individuals in a group crosses a certain threshold, the probability of re-encountering the same individual becomes too low, and the cost of remembering all individuals becomes too high, and thus we should expect large groups such as those of eusocial insects to rely on general class-level cues, such as colony odors

of other types of pheromones.

Another extension would be to break symmetry in the interactions. Our model assumes that interactions are always symmetrical, that is, an agonistic interaction causes both agents to be repelled, and an affiliative one causes both to be attracted. This is not always the case in nature, for instance in societies where hierarchy (which should keep individuals in the group) is maintained by aggressive displays (which would tend to separate individuals in our model). It is also plausible that two individuals interpret the same action in different ways, *e.g.* one individual classifies the interaction as neutral while the other classifies it as affiliative.

Another promising approach is to model different levels of recognition as different strategies in a game-theoretical framework. Game theory is specially suited to investigate fitness payoffs, and it would not be difficult to integrate this approach with other models, such as Reproductive Skew and Resource Dispersion. One possible approach would be to model the evolution of conspecific or offspring tolerance (as in RDH) in terms of strategies, which we expect would match the predictions of transactional models of Reproductive Skew.

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