The evolution of animal societies

Quiñones Paredes, Andres

ENGLISH SUMMARY

Background

Social interactions play an important role in animal life. However, the degree of interdependency between individuals varies vastly from species to species. On the one end, there are species where individual's interactions with their conspecifics are limited to competition for different resources; while on the other side of the spectrum, there are species where individuals require being in a social context to successfully complete their life cycles. Understanding the evolutionary forces behind the vast diversity of social behaviours is the aim of social evolution.

The prominence of natural selection, as the leading mechanism behind evolutionary change, stresses the role of competition between individuals driving the origin of traits in natural populations. Thus, cooperative interactions have been perceived, from a Darwinian perspective, as puzzling, and in need of an explanation. Nevertheless, cooperative interactions are ubiquitous in nature. Social evolution theory has, over the past 60 years, attempted to solve this apparent paradox by describing and analysing abstract and general mechanisms for the evolution of cooperative behaviours.

In this thesis, I build upon that knowledge, and try to use some of those general mechanisms to understand specific biological systems. With this aim, I present a series of evolutionary models that attempt to capture key factors in the evolution of those cooperative systems. First, I present a model about the evolution of human cooperation in the context of cultural evolution. Second, I present two models and field data about the major evolutionary transition from solitary to eusocial life. The models are inspired on the life history of taxa with primitively social species. Finally, I present two models on the evolution of negotiated helping behaviour in the context of cooperative breeding. The models are inspired on the ecology and life-history of a cooperative breeding cichlid.

The cultural evolution of human cooperation

Humans owe their outstanding ecological success partly to their social behaviour. Human societies show an unprecedented level of cooperation in many aspects of their complex dynamics. These cooperative interactions occur among large groups of unrelated individuals. Therefore, the leading theories for the evolution of cooperation, kin selection and reciprocity, cannot fully account for the evolution of

such type of cooperation. The evolution of cooperation through kin selection requires high levels of genetic relatedness among individuals in a cooperative group. Human groups due to their large size and mobility do not fulfil this condition. The evolution of cooperation, through reciprocity, requires individuals to keep track of their past interactions with other individuals; thus, cognitive abilities impose a limitation to cooperation in large groups.

An alternative theory of the evolution of human cooperation is that of cultural group selection. Group selection theory explains the evolution of cooperation by the action of natural selection at the level of the group, rather than that of the individuals. Classical models on group selection have shown that the evolution of cooperation through group selection requires demographic conditions such as small groups and low levels of mixing between the groups. Those classical models, however, assume cooperation to be determined by genes. More recent models, in contrast, assume cooperation to be a cultural trait; that is, is learned from social peers. Some forms of social learning have been proposed to be particularly favourable for the evolution of cooperation through group selection. The idea is that those rules reduce the variation between members of a group, making the differences between different groups more salient and the competition between them stronger. In Chapter 1 of this thesis, we assess this proposition in a systematic way. We develop a computational model where we compare different forms of social learning such as: conformism, leader-following, and pay-off imitation; and, we compare different forms of group competition, to assess which conditions favour the evolution of cooperation. Our results show that conformism, the tendency to copy common behaviours, is less favourable to cooperation than previously proposed. It only allows cooperation to evolve if there is direct competition between the groups, in a war-like scenario. Leader-following, in contrast, has a more positive effect on cooperation in general across the forms of group competition.

The evolution of eusociality

The evolution of eusocial insects, such as ants, bees, wasps and termites, has been described as one of the major transitions in evolutionary history. Major transitions in evolutionary history are events in the history of life that have opened novel avenues of biological novelty. Major transitions share some important features; for example,

many of them involve the origin of a new level of individuality. The evolution of eusociality involves such feature. Individual insects in eusocial species forgo their own reproduction and devote their life to the success of their colony; they also divide labour necessary to secure the colony's success. It is the deep dependency between all individuals in a colony, and the coordinated fashion in which they work, which has led some to call eusocial societies a super-organism.

The evolutionary explanation for why individual insects forgo their own reproduction to invest in the reproduction of their queen was formalized by W.D. Hamilton using kin selection theory. Workers in eusocial colonies give up their own reproduction for the reproduction of their queen, because they are related to her. Thus, she will pass copies of the worker genes to the next generation. Hamilton also provided the first hypothesis to explain the prevalence of eusociality in haplodiploid taxa. Sisters in haplodiploid species are more related to each other than to their own daughters; thus, eusociality is more likely to evolve under haplodiploidy. Therefore, haplodiploidy can be considered a preadaptation to eusociality. Later theoretical work on the haplodiploidy hypothesis showed that considering the male side of a colony cancels the benefit of raising highly related sisters. In chapter 2, we present a series of models inspired on the life-history of taxa with primitively social insects and show that haplodiploidy indeed favours eusociality; however, this is only when a series of other preadaptations, such as monogamy, sex ratio manipulation, bivoltinism and female hibernation, are in place. More interestingly, our model shows that when a solitary species produces two broods in one year, and females can evolve different sex ratios for each one, they evolve to produce a first fully female bias worker brood, and a second reproductive brood with even sex ratios. Thus, our model presents a radical life-history change as part of the evolutionary transition to eusociality.

In the models presented in chapter 2, we assumed that the sex ratios in a colony are determined exclusively by the reproductive females. Several studies, however, have shown that in some cases workers can change the sex ratio produced by the reproductive female. Due to their sterility, they do this by selectively caring for one sex more than the other. In chapter 3, we extend one of the models presented in chapter 2, allowing partial control of workers over the sex ratio of the colony. Furthermore, we allowed reproductive females to have a different sex ratio strategy when they have workers and when they do not. Worker partial control over the sex ratio had a twofold effect: it facilitated the original evolution of sterile workers, and promoted a polymorphic population with solitary and eusocial nests. Furthermore, the flexible strategy in sex ratio caused the evolution of split sex ratios; that is, when some nests produce the females, and others the males. Split sex ratios are found in many species of social insects. Our model, thus, presents a novel explanation for such phenomenon.

Primitively social species are particularly interesting for the evolutionary theory of eusociality. As they have not evolved eusociality so long ago, they allow us to understand the very first changes that species go through during the transition. Even more interesting are species with polymorphisms in social behaviour; as they provide the opportunity to understand conditions under which eusociality is selected for. In chapter 4, we present data on brood care behaviour in a species with polymorphism in social behaviour. We show that reproductive females show extended brood care. They regularly assess the condition of the developing larvae and react to unusual changes that might occur. This finding supports the idea that extended brood care is another preadaptation to eusociality.

The evolution of cooperative breeding

Cooperative brood care, when individuals help others in raising their brood, is a major ecological and life-history decision in the life time of an individual. For helping individuals, cooperative care implies investing time and resources into the survival and reproduction of somebody else's brood; time and resources that could be used for their own reproduction. The logical question is, of course, why would an individual delay her own reproduction to aid a peer? Traditionally, the answer to this question was in terms of kin selection theory. An individual delays her reproduction to help her kin, indirectly favouring the transmission of her own genes. Recent years, however, have seen the accumulation evidence for biological systems where individuals delay their reproduction to help unrelated individuals. Thus, an alternative explanation to kin selection is necessary.

One of the examples of systems of cooperative breeding among unrelated individuals is the cichlid *Neolamprolagus pulcher*. In *N. pulcher,* dominant individuals tend to

monopolize reproduction, and subordinates of different sizes divide the necessary tasks for nest maintenance and brood care. Experimental evidence shows that subordinates use helping and submissive behaviours to appease aggression from dominants. On the other side, dominants adjust their level of aggression according to the help received. It seems that helping behaviour in *N. pulcher* evolved as a payment of rent from subordinates to dominants for the right to stay at a territory that provides fitness benefits. As part of the decision of whether to evict lazy subordinates there is a negotiation between the partners. In chapter 5, we present an evolutionary model, inspired by the ecology and life history of *N. pulcher,* where we include an explicit negotiation between a dominant and a subordinate. Our model shows that helping behaviour can indeed evolve as rent payment when individuals negotiate the final level of help and aggression they give. Moreover, when we include genetic relatedness between the partners the dynamics lead the partners to two alternative outcomes. One of these is achieved through the negotiation between the partners, as when relatedness was absent. The alternative equilibrium is driven by kin selection, where subordinates provide help without being forced to, and the dominants do not behave aggressively toward subordinates. Interestingly, the negotiated solution yields a higher level of help than the kin selected solution. This means that despite the general positive effect of relatedness on helping behaviour, in this system, relatedness reduces the average helping level achieved by populations.

In chapter 6 we present a general model of negotiation between partners inspired by the specific model presented in chapter 5. Mutual responsiveness is a much more general phenomenon than the example of cooperative breeding analysed in chapter 5. The general model makes no assumptions about the ecology or life-history of the negotiating partners, or about the mechanism through which individuals respond. We derive conditions for the evolution of the responsive behaviours, as well as equilibrium conditions. Furthermore, we derive stability conditions for the potential equilibria. Interestingly, the shape of the reaction norms determining the response of individuals has strong implication in the stability of evolutionary equilibria. This result points to the importance of looking into de mechanisms of responsiveness, as they could determine when negotiation solutions are a possible evolutionary outcome.