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Evaluation of Michael Chimento's PhD Thesis: "The influence of social processes and structures on cultural evolution"

This thesis employs and integrated experimental and theoretical approach to investigate a fascinating aspect of animal behavior, cultural transmission of social information, employing a model bird species, the great tit. It begins with a well-written and comprehensive overview of social learning and evidence of 'culture', in non-human animals. The various mechanisms by which social learning can occur, and how this may be impacted by, and in turn impact, evolutionary processes. In addition, many fascinating examples of social learning are given as well as a discussion of the conditions under which social learning may, and may not be, adaptive. The experimental literature for cultural selection in non-human animals is particularly informative and allows the reader to understand clearly where this thesis fits in, and importantly goes beyond, what was previously known. Following this the candidate turns to a useful methodology for the analyses of social behavior, graph theory. The role of social networks in animal behavior research is summarized briefly, including dynamical aspects and features that impact social networks over different spatial and temporal scales.

In Chapter 1, an experimental study of the role of population turnover on cultural selection in birds is presented. Employing manipulative studies on 18 captive populations of great tits it is shown that a gradual influx of naive birds increased the probability that a more efficient behavior—in terms of solving a puzzle box—could arise, and persist. Indirect, but strong, evidence is presented that birds learn socially and automated identification of birds at the boxes provided a detailed record of close temporal (and thus spatial) associations among birds. Naive birds were found to more likely sample the more efficient solution to the puzzle box, whereas residents were canalized by their previous experience with less efficient solutions. This resulted in immigrants amplifying efficient social information, making efficient solutions faster to establish in populations. This appears, at first, reminiscent of the utility of stochasticity in biology more generally, such as in simulated annealing, noise (as long as not too strong) allowing escape form suboptimal local solutions, and also the role of 'uninformed' bots in online collective decision-making, which if not too plentiful, allow the population as a whole to find better solutions. However, here evidence is presented that the mechanism actually relies on immigrants disproportionately adopting efficient behaviors from residents, although I wonder whether stochastic effects introduced by naive individuals plays some role. Much to think about! This is also discussed in detail in the paper with reference to relevant previous work - the difference is that the present experimental design is more able to reveal the underlying mechanism and the mechanism discovered is both novel and, at least for me, relatively unexpected. It is a fantastic chapter.

Chapter 2, which I note has recently been published in Proceedings B, turns attention to a theoretical study of how information production may influence diffusion dynamics in social networks. While the abstract explains the concept, and that they "find that the influence that production rules have on diffusion dynamics have consequences", we don't get told what these consequences are, nor what the results are! It may well be that your "model illuminated the differences between social learning and social influence" but the reader is less illuminated unless they read the paper - It would have been good to have the main results in the abstract, not just the main concepts. My only other (very minor) gripe is where, in the introduction, 2 examples are given of 'social learning'. The first is learning of a novel skill "such as a cockatoo learning to open bins from associates". I agree, this is learning. However, the second is "the influence that social information exerts upon behavioral choice, such as when a stickleback fish chooses feeders surrounded by more conspecifics". This second example, however, does not imply anything about learning. Individuals in many special species bias decisions by sensory information regarding conspecifics, but such responses can be fully explained without any learning; for example, this is an innate response in fish. The paper referred to does, however, consider learning - so it's just a lack of information in the description I suspect. However, I see this in a lot of papers - where people use "social learning" when they really should use "social information" or "social cues". Anyway, this is just a very minor point, and the n the example is expounded upon it becomes clear what is meant.

I very much like the discussion of the circular relationship between acquisition and production. I think this is all-too-often overlooked, and as the candidate writes, this "can also lead to ambiguity over the precise target of causal factors that influence cultural evolution". This also gives a very nice justification for the utility of modelling these processes, the focus of this chapter. While a verbal argument is given why population size may not matter, it would have seemed to have been easy to evaluate whether the intuition that it only results in longer diffusion times, so I'm a little confused why that was not just done. But again, a very minor issue - the candidate is most probably correct. The results are well-presented, and as I wrote above evaluating both production and acquisition is really important. The discussion states that "In doing so, we have uncovered new predictions for how changes to learning rules affect cultural diffusion dynamics by altering the relative competitiveness of novel behaviors", but we are not told what these predictions are. The reader has to work pretty hard to find what is meant here and what the predictions are - this would have been good to explain directly (they are rather obfuscated in a series of biological examples). This isn't helped by the main conclusions not having been drawn in the abstract. So, overall, while I find this really strong scientific work, it could have been better communicated.

Chapter 3 turns to optional turnover regimes, the theme of the opening data chapter. As in the previous chapter, the abstract has some tantalizing information, including "that there are optimal turnover regimes that promote selection for higher payoff behaviors" and that "the optimal network regime depends on network size, density and how easily the behavior can be socially learned by agents". Brilliant - but in what way? How does it depend on these things? Does optimal turnover increase or decrease as a result of these factors? Again, this is fantastic science, but the abstract explains that there are results, and what they depend on, but not actually what they are.

The Introduction to this chapter is excellent. As in the previous chapter he has picked up on major gaps in knowledge and well-justifies the purpose of this work. I am a bit confused about the ordering of the thesis chapters though. This work aims to predict how turnover rate might affect cultural evolution, and is effectively a model creating predictions for what is tested experimentally in Chapter 1. Thus, it is strange, to me at least, why it did not precede that chapter, or at least follow it directly. At the end of the Introduction, it is written "These changes could lead to positive, negative or neutral consequences for the relative proportion of adaptive

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behavior that a population used, compared to static populations." - again, it would be great to know what features result in it being positive, negative or neutral, not just that it can be.

The results are really great, and also the counter-intuitive effects very well explained, such as *why* the proportion of low-payoff monomorphic agents began to rise. These are exactly the sorts of clear explanations for the interesting results that one needs to best enjoy this fantastic work. Again, we find the same later: "Fast tempos were most detrimental in small networks, sparse networks, and for behaviors which were difficult to socially learn. Large networks, dense networks and easily learnable behaviors all increased the number of turnover regimes that a population could undergo without negative performance compared to static populations. Additionally, the benefits of optimal regimes improved under these same conditions". Fantastic explanations of the results - a shortened version of that could have well-suited the abstract. And this continues with "There were two underlying reasons for these effects. Network size determined the amount of memory available within a population." - again, really fascinating results. The Discussion is also great. I love this work - it off of extremely high quality - but given the prediction "that naive individuals can drive the cultural evolution of efficiency simply by being "better" samplers", this would have been terrific to have prior to the experimental test to really bring home the thesis of the thesis.

Chapter 4 addresses whether animals utilize social information to differing degrees as a function of spatial and/or temporal variability in environment. In this integrated experimental and theoretical chapter, the candidate replicates the types of experiments that have previously shown a short-term change in social learning in primates and humans. Here, the abstract is excellent, explaining the concept, and most importantly what the findings are. The chapter makes great use of the experimental paradigm developed for great tits and investigated symmetric and asymmetric environments (i.e., the same, or different, environments to their original population, respectively). In addition to the experiments a model was developed to aid understanding - such as to ask whether immigrants who began rot prefer the resident-side solution were more likely to have been influenced by the social information provided by residents, or independently switched strategy. It is a very clever experiment as they can independently investigate the role of changes in environmental cues and/or the payoff landscape, and the flexibility of birds to alter their social learning strategy in response to different types of uncertainty. In addition, unlike previous work, it shows a subtle difference between transmission bias and production bias, a distinction which appears to have been overlooked in many previous studies. Given that these birds live in fission-fusion populations, the effects shown in studies such as these (which can occur over the relatively short term) are likely to be highly-informative to make predictions in the field. Excellent work.

While Chapter 3 largely focused on other aspects, Chapter 5 explicitly considers the role of social network, architecture and how it influences the tempo of cumulative cultural evolution. They look at the rate of "cultural recombination events" and the possibility of having multiple parallel cultural lineages - all key issues to address in this exciting field. A main finding is that no one type of social network architecture consistently promotes cumulative cultural evolution, but that details, such as population size, interaction density and diffusion mechanisms, matter, and sometimes can reverse effects. In addition, they use their results to question the hypothesis that multi-level, structured societies may be predisposed for cumulative cultural evolution just by virtue of that network topology. In addition, highly structured network topologies could result in cultural loss if connectivity cocoons too low for new innovations to spread effectively, and also that while multilevel, networks promote fast recombination, it can then restrict the spread of higher-value cultural traits. Overall, very nice and interesting results. The chapter is also well written and well-presented throughout.

Chapter 6 investigates complex foraging behaviors in wild birds and how they emerge from social learning and recombination (a great ordering this time!). Taking advantage of an

experimental design that necessitates a 2-step process they can investigate how skills can be recombined to solve more complex problems. Very cool! Particularly interesting is the finding that social learning appears to be particularly important for learning each component, but that combining them together may occur predominantly at the individual-level, i.e., asocially. Unlike the previous chapters, this work was conducted directly in the field - thus the thesis as a whole shows the considerable power afforded by both smart lab-based research, and taking these ideas into the wild. I really like the result that complexity can emerge from social learning of relatively simple features and then 'combining' within individuals. I suspect this may be relatively ubiquitous, and this work likely sets the scene for many follow-ups.

The final work, in Chapter 7, expands to consider cumulative culture across species, and in particular the role of efficiency. Efficiency here is framed in terms of genetic fitness (i.e., at the individual level) and form the perspective of the behavior itself (e.g., learnability). There is a lot to like about this chapter - it is a deep topic and inherently very thought provoking. The arguments made could have been lost in this complexity, but are not. This is a chapter that I am going to have to read again, and more than once, because there is so much it brings to the table. What a wonderful way to end the thesis with such a thought-provoking and bold work!

Summary

Overall, this is one of the best theses I have ever read. It integrates deep thinking, extremely clever experiments and likely more than one shedload of hard grind, to create a body of work that the candidate should be truly proud of. It is exceptional.

Grade: 0

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