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April 10, 2021

Prof. François Munoz
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Dear Prof. Munoz:

Thank you for serving as recommender on this manuscript. The reviews were excellent, and I think the manuscript is much improved. They prompted two substantial changes:

First, there is a new section describing simulations with mixed strategies. These simulations confirm the instability of the Nash equilibrium (NE) and show that, in spite of this instability, the process tends to stay in the neighborhood of the NE when the opportunity cost or the number of competitors is large. I expressed this as a conjecture in the previous draft but now present it as a result.

Second, I have removed appendix B of the previous draft, which asked when a mixture of mixed types could be an ESS. This appendix seems unnecessary, because the NE in this game is not an ESS. If you or the reviewers think it is needed, I will be happy to restore it and strengthen the argument.

The other changes are described in the detailed responses below.

Yours

Alan R. Rogers

Detailed responses. (Reviewers' comments in *italic type*, my responses in roman.)

Munoz

1. *The 3 reviewers noted that the reference to Maynard-Smith is not most suited and/or can be somewhat misleading. They suggest referring to the Bishop-Cannings theorems.*
   Done.
2. *In addition, stating that foraging ecology has little to say about game theory would be exaggerated. Some references are proposed for the later point.*
   I have removed the paragraph about classical foraging theory.
3. *Another important point is whether and how the maths, the simulations and the lab experiments together support the main point of the paper on the evolutionary trajectory to mixed strategy. Apparent inconsistency between analytical expectation on non-stability and observed "approachability" in simulations needs further explanation and discussion.*

In response to this comment, I have added a new section (4.2, "Simulations with mixed strategies."). It describes simulations in which two random mixed strategies compete with each other and with the Nash equilibrium (NE) strategy. These simulations confirm that the Nash equilibrium is not an ESS. Furthermore, they show that when either the opportunity cost or the number of competitors is large, the process tends to stay in the neighborhood of the NE, even though that equilibrium is evolutionarily unstable. This was a conjecture in the previous version of the manuscript, now I report it as a result, and I have revised the introduction and discussion accordingly.

I looked at the literature on approachability (beginning with Blackwell, 1956), and I can see that it might be relevant. However, I don't understand it well enough to be sure. Blackwell's theory is about zero-sum games, and "berry patch" is not zero sum, so the relevance is not obvious.

4. *Regarding the lab experiment, I share the concern that the model assumptions and the specific experimental conditions should be cautiously discussed. It would be misleading to suggest that the experiment demonstrates or even illustrates the theoretical results without discussing the limitations of such comparison.*

   The discussion of this comparison has been rewritten and now acknowledges differences between the model and the experiment. It also points out that agreement between model and experiment need not imply that human behavior has been shaped by the evolutionary process described in this manuscript.

5. *The point by reviewer 1 that the model could be analyzed in a context of Adaptive Dynamics also needs discussion.*

   See below.

Anonymous reviewer

6. *It is however not exactly true to write that foraging ecology has little to say about game theory. Maynard Smith models (e.g. Hawk dove) can be interpreted as foraging models. Also, Bulmer (Theoretical Evolutionary Ecology, p168) discuss and analyzes a foraging model.*

   I have removed the paragraph about classical foraging theory.

7. *What strikes me is that the fact that the mixed strategy was not found to be evolutionary stable in the analytical treatments but was found to be "approachable" in the simulations. To me, this is an important caveat in the ms and questions the role of the analytical treatment. Is the mathematical treatment relevant with regards to biology?*

   This comment is addressed by the new section (4.2) on "simulations with mixed strategies," which is discussed above. I would argue that the analytical treatment is relevant, because it specifies the Nash equilibrium, and the unstable dynamics remain close to that equilibrium under conditions that I specify. The Nash is therefore predictive in spite of its evolutionary instability.

8. *Second, it is always interesting to confront experiment and theory but to me, it seems premature to interpret the classroom experiment in the light of the model. I also found risky to interpret ecological or ethnographical examples in the light of a model whose dynamics is not totally understood.*

   Perhaps this concern is now moot, because the new analyses have made the dynamics less mysterious. Nonetheless, the discussion of experimental results has been revised (see above) to address this concern. I don't think there is really any problem with the ethnographic examples, because I use them only at the beginning of the manuscript, to motivate an interest in the question. I don't present data from these ethnographic contexts, and I don't claim that these examples are consistent with the model. In the new draft, they are not mentioned after the introduction.

9. *In an historical perspective, the hawk dove model is a sort of metaphor that can help to interpret empirical patterns. In the present case, the ms oscillates between a sort of mechanistic model (close to ecological mechanism) and heuristic model.*

   The discussion has been rewritten to emphasize that the model's qualitative conclusions are of more interest than its numerical ones and that it is useful as a metaphor.

François Massol

1. *The book of Maynard Smith is cited at various locations in the ms to justify the payoff equality between pure strategies at the NE (or potential ESS). However, this result is classically known as one of Bishop-Cannings theorems (Bishop and Cannings, 1976).*

   Done. (I cited their 1978 paper, which includes the same theorems.)

2. *Also, in the same vein, section 3.3 and appendix B could make use of the term "evolutionarily stable coalition" instead of the vague "evolutionary equilibrium". The use of "coalition" in this context was probably first introduced in the literature by Brown & Vincent (1987), to the best of my knowledge. Other useful references from the 80's theoretical biology literature could also be read on this topic (Thomas, 1984, Hines, 1987).*

   As Brown and Vincent (1987) define the term, and evolutionary stable coalition is a set of strategies whose frequencies converge to stable values. In the berry patch model, the frequencies of the various mixed strategies are always in motion. This seems more similar to the situation described by Hines (1980, J. Appl. Prob. 17:600), in which there is an evolutionarily stable state, consisting of multiple mixed strategies, whose frequencies continue to drift at random. The berry patch is different however because it lacks an ESS, and there is no convergence to a state at which all remaining variation is neutral.

3. *For the reader more knowledgeable about evolutionary ecology models than game theory fundamentals, it looks like the model could be amenable to an adaptive dynamics (AD) analysis (Hofbauer and Sigmund, 1990), i.e. considering v, or some characteristics of the distribution of v (i.e. its expectation, variance, etc.), as an inheritable trait and looking at the selection gradient for this trait, considering payoffs as a proxy for evolutionary fitness (i.e. the number of offspring sired given the strategy of the parent).*

   This is a good idea, but it would be an entirely new paper. It's more than I would want to undertake in this revision.

4. *Using mutational processes closer to those classically used in AD (instead of the ones described on page 8) might also help.*

   The reviewer is referring here to the mutational model in the simulations in section 4.1: mutants adopt a new strategy that is chosen at random. The purpose of these simulations is to show that the theory is correct. I think it would undermine this purpose to use the mutational model of AD.

   The problem is that AD uses a "smart" model of mutation, which perturbs a mutant's fitness in a direction that increases its fitness. Were I to use such a model, one might worry that the agreement between simulation and theory was produced by the mutational process itself, rather than by selection. This is not an issue in the current simulation, because the mutational process is random and cannot account for the agreement between simulation and theory.

5. *To understand what happens in the classroom experiment, would it be possible to invoke risk aversion and the necessity, in real-life situations, for the game to be repeated? If long-term fitness depends on the geometric average of payoffs gained through such games, it might be advantageous to limit losses, more so than trying to obtain the best average gains. Or conversely, one might consider than v's less than c could emerge out of spite (if e.g. a player had been beaten in an earlier game)? More generally, the presentation of the mathematical model begins with astute considerations regarding the application of a one-shot game; it would be quite useful to get such considerations back on the table when discussing the interpretation of the discrepancies between classroom experiments and the analytical model. Repeated games, as well as more realistic situations involving relatedness among competitors (with consequently closer than expected strategies), might affect the evolutionary outcome.*

   The new draft mentions these possibilities in discussing the experiment. However, it goes on to argue against such interpretations. The problem is that populations should never be at the NE, because it is unstable. They should often be near it, but even then, the NE will not provide a precise numerical description. For this reason, I argue that the model's qualitative predictions are of more interest than its quantitative ones. In qualitative terms, there is good agreement between the experimental data and the NE.

6. *Maybe at some point it might be interesting to point assumptions that are ecologically questionable (since PCI ecology is about ecology in the first place). I'm thinking e.g. of the fact that choosing v might be less simple than choosing the time to harvest resource; if the two quantities are not 100% linearly correlated, this can create enough stochasticity to select for more prudent strategies. The cost of acquiring information might also come into play (at least in the form of a non-constant opportunity cost "the longer I wait, the more time I could have spent fishing"). Finally, ecologically realistic situations probably involve the existence of multiple berry patches and a handling time for picking berries, which might limit the opportunities for too strong inequality in payoffs among competitors after one season. Overall, all of these assumptions question some of the applicability of the present model. All models are wrong, so this does not bother me that much, but at least it is better to present all of these points and go through them and their potential consequences for the study results, rather than ignore them altogether.*

   The discussion now begins with a paragraph that acknowleges some of the ways in which reality is more complex than the current model.

7. *I was wondering whether it could be possible to look at what happens when ties are not exact. In other words, the experimental part of the study states that ties divide the gain equally between all competitors that chose the right time for harvest; in the analytical part, this rule is not useful because time is considered continuous and players are assumed to play mixed strategies, but what would happen if sufficiently close decision times occurred? (i.e. if A acts at time t and B acts at time t + epsilon, how should the bounty be split, assuming the time to pick all the berries is larger than epsilon?) Would this additional rule solve the paradox of the non-evolutionarily stable NE? Again, this is more like a suggestion, but some bizarre model results sometimes do not resist the addition of more realistic assumptions.*

   Agreed. In the first paragraph of the Discussion, I now point out that the unrealistic features of the model may account for its instability.

8. *Equations (9-13) are not commented, or barely. It could be useful e.g. to assess whether Q increases with K, c, etc. And the same thing for, $\bar{v}$, Π, ... This absence of comment is especially acute when one arrives at the top of page 11, where comments on functions are at last given—the reader is then left wondering whether the same exercise would have been possible earlier, i.e. on equations (9-13) rather than equations (16-19).*

   The questions raised here become interesting only after we know that the mixed equilibrium exists and is (at least in some circumstances) stable. In the earlier set of equations, we don't yet know that the mixed equilibrium even exists, so interpretation would be premature.

9. *You should give a more substantial legend to Table 1, probably incorporating all of footnote 1 to explain what D means.*

   I deleted the table and all mention of D.

10. *In Figure 6, the legend is not self-sufficient (the values of K, c, are missing). Also the x-axis scale (between 0 and 10) is weird at this point in the text. One has to get back to the way the classroom experiment is written to remember why there is this difference.*

    I have clarified the caption of this figure.

11. *The use of "unstable" instead of "evolutionarily unstable" is a bit problematic sometimes because the two forms of stability (classic dynamical system stability and evolutionary stability) can be studied together in models like this one.*

    The manuscript now refers consistently to evolutionary stability and instability.

12. *In the integrals of equation (22), v is both the upper bound of integration and the variable to integrate over. You should use two different symbols.*

    Fixed.

13. *The reasoning between, inequality (23) and $Q > 1/2$ is not obvious. It involves a little bit of analysis. Since this is an appendix, you might as well write it down (briefly).*

    I have added a paragraph deriving this result, and I can't imagine why I left it out to begin with. Reminds me of the famous "then a miracle occurs" cartoon.

14. *The transition just after equations (24-25) reads "adding and subtracting c", but in reality you immediately recover these equations by using $Q = 1$ – the integral of f and distributing the integrals.*

    I have reworded that sentence as the reviewer suggests.

15. *On pages 15-16, showing that D is maximum for $J = I$ is actually quite stronger than proving that it is not an ESS — it means that all other mixed strategies can invade! Maybe this should be discussed a little.*

    I agree this is remarkable, but I don't really have anything more to say.

16. *The "Euler equation" is strange. Given the writing of Z as a function of s of v, I would use d/du rather than d/dx for the derivative with respect to the integrated variable. And you can also find this result using the same integration by parts trick used later to find the second derivative of D. You might as well explicit this computation directly.*

    I think the reviewer means d/dv rather than d/du. This problem is now fixed.

17. *Condition (27) is also true for a NE, so if the starting point of appendix B is a NE, you don't have to prove that condition (27) is true, do you?*

    Appendix B no longer exists.

18. *But I don't find your justification at the top of page 18 very convincing—to me this does not answer what happens when mixed strategies J try to invade, i.e. whether $\Pi(J, I^K)$ are equal*

to $\Pi(I, I^K)$. *Using equations (31-33), however, helps you to prove it (you simply have to compose the* Π *score based on those of all pure strategies).*

I agree about the weakness of that paragraph. But fortunately, the issue is now moot, because the weak paragraph was in appendix B, which no longer exists.

19. *I'd say that the factorisations you propose (equation [29] and the ensuing equations [31-33]) are OK if the random variable* X *yielding the actual pure strategy chosen by any player is not correlated to any other "environmental" random variable, i.e. if players do not synchronize their strategies through some external signal. Otherwise, you would have to condition* B^K *by* I *playing* x *in equation (31), i.e. the choice of the pure strategy chosen by the focal should partly determine the population of pure strategies it will play against. There might be some formal way of expressing this condition using correlations / independence of the various random variables.*

    This refers to appendix B, which no longer exists.

Jeremy Van Cleve

20. *In determining the mixed strategy on page 6 after eq 8, the author cites Maynard Smith for the result that pure strategy playing against the mixed strategy ESS I obtains the same payoff as I playing itself. In fact, the author should cite Theorem 1 from Bishop & Cannings (1978, JTB), which is what Maynard Smith cites.*

    Done.

21. *Theorem 3 from Bishop & Cannings says that mixed strategy ESSs cannot completely overlap in their support, which implies that the mixed-strategy* I *in fact must be the unique mixed strategy since it's support is* $(c, 1)$.

    Because B&C state their result in terms of ESSes, it is not obvious that it applies to the berry patch game, which has no ESS. As I read their proof, however, it does not refer to the "second-order condition" of the definition of an ESS, as the reviewer points out in the paragraph that follows the one I quoted above. For this reason, it should apply to Nash equilibria that are not evolutionarily stable. But since B&C don't say this, I can't really cite them without further explanation.

    I'm sure, however, the reviewer is right about this NE being unique. I derive the NE (equations 9–11) from the consideration that $d\Pi(v, I^K)/dv = 0$ if I is a mixed NE. If there were more than one NE, this equation would have more than one solution.

22. *The results in A.2 however suggest that* I *is not only unstable but is in fact a minimum and is always invadable by a nearby mixed strategy. I couldn't find nothing wrong with the analysis and I don't know what to suggest here, but my guess is that the mixed strategy isn't always a minimum.*

    The NE can't be a global minimum, because it resists pure-strategy invaders when $Q > 1/2$. This is not surprising, because there are limitations to the argument showing that the NE is a minimum. My argument assumes that invaders go fishing with the same probability as the NE, and I haven't considered discrete mixtures such as "go fishing with probability p, and otherwise play $v = 1$."

23. *The experimental data were suggestive that the mixed strategy is predictive but having groups of different sizes would help determine more robustly how much student players replicated the model predictions.*

Agreed. Perhaps I can interest an experimentalist into collaborating on such a project.

24. *I suspect the author should also include additional experimental information (such as how subjects are recruited, any demographic information, etc) and any necessary IRB information.*
    Done

25. *Equation above equation 12: you could just say that* $\Pi(1, I^K) = Q^K = c/U$.
    Done.

26. *Page 8: "dynamically stable". Define this.*
    This passage has been deleted.

27. *Page 11: Isn't* $Q_K = Q^K$*? This might be mentioned.*
    It's Q^{K+1}, because there are $K+1$ individuals in each group. I've added that to the equation defining Q_K.

28. *Table 1...*
    This table has been deleted along with the accompanying text.

29. *Page 14: "definition of I implies that* $\Pi(J, I^K) = \Pi(I, I^K)$*." Yes but this goes to the heart of where Bishop and Cannings Theorems 2 says that a mixed ESS can't be completely contained in another the support of another ESS.*
    I see how this sentence relates to B&C's theorem 1 (which I now cite), but I don't understand the connection to theorem 2.

30. *Page 16. The second line of the equations following "Integrating by parts produces..." has an integral symbol missing the lower bound c.*
    Fixed.