

Dept. of Anthropology  
260 Central Campus Dr., Rm 4428  
Univ. of Utah  
Salt Lake City, UT 84112

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Prof. François Munoz  
PCI Ecology

Dear Prof. Munoz:

The second set of reviews identified several points that needed clarification, and I have revised the manuscript accordingly. I did not however agree with the major points in Prof. Massol's review, which argued that my section 3.3 is neither necessary nor correct. I will contest both points below.

I'm grateful to you and to both reviewers for your efforts on this manuscript.

Yours



Alan R. Rogers

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

### **François Massol**

1. *in reality, there cannot be any NE consisting only of pure strategies. To realize that, imagine that  $A$  players have gone fishing and  $K + 1 - A$  have chosen a variety of  $v$  values. Obviously, any one of the  $K + 1 - A$  individuals that has not chosen the smallest  $v$  could have done better by going fishing. So now imagine that  $A = K$  and thus only one player tries to harvest. If it has strategy  $v > c$ , then all fishermen can do better by choosing any harvesting strategy between  $c$  and  $v$ , and the harvester can always do better if  $v < 1$ . So there can't be any NE consisting only of pure strategies, except for the very trivial one (everybody but one player going fishing and the last one harvesting at  $v = c$ ).*

I agree and have changed that passage as the reviewer suggests. Point of clarification: the one exception that the reviewer mentions isn't really a NE either, because the individual playing  $v = c$  could do better by playing  $v > c$ .

2. *What is proved in 3.2 is that we can find a mixed strategy that is an ESS, using BC theorem to find it.*

I see this differently. A mixed ESS must satisfy two conditions. As Bishop and Cannings (1978 JTB 70:85, equation 3, p. 90) stated these for pairwise games,

$$\Pi(I, I) = \Pi(J, I) \quad \text{and} \quad \Pi(I, J) > \Pi(J, J)$$

Section 3.2 of my own manuscript describes a strategy ( $I$ ) that satisfies the equality condition

but does not discuss the inequality and therefore does not demonstrate that  $I$  is an ESS. It shows only that  $I$  is a Nash equilibrium, not that it is an ESS.

3. *The point that section 3.3 is trying to insert is not a useful one: resisting invasion in game theory means being an ESS. Since the strategy defined above is an ESS, it does resist invasion by others.*

Section 3.3 addresses an essential point. We cannot decide whether  $I$  is an ESS without evaluating the inequality in equation 3 of Bishop and Cannings (1978 JTB 70:85), which is analogous to my inequality 14. Section 3.2 does not do this; section 3.3 does.

Furthermore, section 3.3 shows that  $I$  is *not* evolutionarily stable, and this mathematical result is confirmed by computer simulation. Figures 6 and 7 would be incomprehensible if, as the reviewer claims,  $I$  were an ESS and section 3.3 were incorrect.

4. *The problem with section 3.3 is that it is based on the prologue of appendix A, which tries to compare  $w_J$  and  $w_I$  based on the probability that  $I$  or  $J$  encounters groups of  $I$  only or with the inclusion of one  $J$ . However, this is a very bad reasoning: Imagine that  $J$  is rare and say we are looking at the probability that the group of players will count 0, 1 or 2  $J$  players (to make things simple). Let's call these probabilities  $k_0$ ,  $k_1$  and  $k_2$  (attention: these are probabilities of encountering the whole group, not its individual players). Now let's call  $P_0(I)$ ,  $P_0(J)$ ,  $P_1(I)$  and  $P_1(J)$  the respective probabilities for an  $I$  player to compete against  $K$   $I$  players, for a  $J$  player to compete against  $K$   $I$  players, for an  $I$  player to compete against 1  $J$  and  $K - 1$   $I$  players, and for a  $J$  player to compete against 1  $J$  and  $K - 1$   $I$  players. Given the  $k_i$ s defined before, we obtain:  $P_0(I) \propto k_0$ ,  $P_0(J) \propto k_1$  (the group needs to have exactly one  $J$  player),  $P_1(I) \propto k_1$  (you need to find exactly one  $J$  player to compete against)  $P_1(J) \propto 2k_2$  (you need to find two  $J$  players, one for the focal and one for the unique  $J$  opponent, and since players are not labelled there are two combinations of this configuration for each group containing two  $J$  players) As you see, the  $P_0$  of  $I$  and  $J$  are not the same. And the  $P_1$  of  $I$  and  $J$  are also completely different. . . . So the whole reasoning presented at the beginning of appendix A is false. But this is not a problem since what it was trying to reproduce in the first place is the ESS reasoning that you have already performed!! (and which proves that  $I$  is an ESS)*

I agree that in a finite population  $P_0(I) \neq P_0(J)$  and  $P_1(I) \neq P_1(J)$ . However, I will argue that the differences between these quantities are small in large populations and disappear in infinite ones. My manuscript ignores effects of finite population size as is conventional in evolutionary game theory. In what follows, I will focus on  $P_1(I)$  and  $P_1(J)$ . The argument for  $P_0(I)$  and  $P_0(J)$  is similar, but I won't detail it here. Like the reviewer, I will assume for simplicity that individuals compete in randomly-formed pairs. This makes my inequality 14 identical to the inequality condition of Bishop and Cannings, which I cite above.

In a population of size  $N$ , suppose that  $x$  individuals play  $J$  and the rest play  $I$ . The probability that an  $I$ 's opponent is a  $J$  equals  $P_1(I) = x/(N - 1)$ , because that is the fraction of  $J$ s among the remaining  $N - 1$  individuals. But if our focal individual is a  $J$  rather than an  $I$ , this probability becomes  $P_1(J) = (x - 1)/(N - 1)$ .

In the reviewer's notation, an  $I$ 's opponent is a  $J$  with probability

$$P_1(I) = \frac{k_1}{2k_0 + k_1} \tag{1}$$

and a  $J$ 's opponent is a  $J$  with probability

$$P_1(J) = \frac{2k_2}{k_1 + 2k_2} \tag{2}$$

The reviewer claims that  $P_1(I) \propto k_1$ , and  $P_1(J) \propto 2k_2$ . But this is not so, because the denominators of (1) and (2) are different. The  $k_i$  can be expressed in terms of  $x$  and  $N$  as:

$$\begin{aligned} k_0 &= \left(\frac{N-x}{N}\right) \left(\frac{N-x-1}{N-1}\right) \\ k_1 &= 2 \left(\frac{x}{N}\right) \left(\frac{N-x}{N-1}\right) \\ k_2 &= \left(\frac{x}{N}\right) \left(\frac{x-1}{N-1}\right) \end{aligned}$$

Substituting these into Eqns. 1 and 2 gives

$$P_1(I) = \frac{x}{N-1} \quad \text{and} \quad P_1(J) = \frac{x-1}{N-1}$$

just as in the simpler argument above. In the limit as  $x$  and  $N$  increase without bounds while  $x/N$  remains constant, these probabilities approach the same value,  $x/N$ . In my appendix A, I ignore the distinction between  $P_1(I)$  and  $P_1(J)$  as is appropriate in a model of infinite population size. I have added a footnote that points this out.

This approximation also underlies the classic result of Bishop and Cannings (1978 JTB 70:85, equation 3) and is standard in evolutionary game theory. The reviewer is thus arguing not only against me, but also against Bishop, Cannings, Maynard Smith, and all the other game theorists of the last half century.

5. *Just to convince you completely, there is also the argument of the quantities to compare:  $\Pi(I, J^1 I^K)$  vs.  $\Pi(J, J^1 I^K)$ . If  $K = 1$  (i.e. there are only two players per arena), then the comparison turns out to be  $\Pi(I, J)$  against  $\Pi(J, J)$ . How can such a comparison inform us about the invasion of  $I$  by  $J$  (since  $\Pi(J, J)$  is about the still non-existent case in which two rare-strategy players would compete against each other)? In fact, this is touching the crucial part: the comparison induced by BC theorem (i.e.  $\Pi(J, I^K)$  vs.  $\Pi(I, I^K)$ ) is the only one that counts when  $J$  is rare.*

This comparison becomes important when  $\Pi(J, I^K) = \Pi(I, I^K)$ , as is the case when  $I$  is a mixed equilibrium.

6. *In the simulations, you mention the existence of “oscillations” when  $2^K * c < 1$ . However, since the points raised by appendix A are now moot, I guess this effect has more to do with the question of invaisibility by  $I$ : given a mixed strategy  $J$ , close to  $I$ , can  $I$  invade? (see Eshel 1983 on the CSS criterion)*

From this point on, the reviewer offers suggestions about how to rescue the manuscript from the problems identified earlier. I have not followed these suggestions because (as discussed above) I don't think the problems are real. Nonetheless, the reviewer's suggested approach sounds interesting, and I hope he will let me know if he makes further progress.

## Jeremy Van Cleve

7. *page 11 “dynamics may be chaotic.” Given that its notoriously difficult to distinguish deterministic chaos from stochastic time series, I think its safer to attribute the noise in the time series simply to stochasticity, which is of course definitely present.*

Good point. That passage now reads:

Although there are no obvious cycles, it is impossible to tell whether the dynamics are cyclical or chaotic. Cycles may be obscured by the stochasticity of the simulation.

8. *In the response, the author that “AD uses a “smart” model of mutation, which perturbs a mutant’s fitness in a direction that increases its fitness”. This isn’t true. Mutations are often assumed to have a normal distribution around the resident trait value and its the selection gradient that creates the deterministic trajectory in the direction of increased mutant fitness. I mention this because one could, as Dr. Massol suggests, use AD to see quantitatively just how the mixed strategy evolves. This kind of analysis might be the place where cycling could be observed.*

I suspect this is a good idea, but I lack the expertise.

9. *On point 29 of the response, I want to clarify what I meant in my previous review if its of use. Theorem 2 of BC78 says that for two mixed strategy ESSs, one can’t be contained within the support of the other. My comment refers to their proof on page 113, which uses Theorem 1. Then Theorem 2 powers Theorem 3.*

Thank you. I see how this works.