Universidad del Desarrollo
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COOPERATION IN SOCIAL DILEMMAS: BIOLOGICAL FOUNDATIONS AND CONTEXT-DEPENDENT SOCIAL NORMS

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DEDICATORIA

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I. RESUMEN

Este trabajo explora factores biológicos e institucionales que afectan la cooperación humana utilizando la aproximación de la economía experimental. Incluye dos artículos publicados, el primero titulado "*No association between genetic variants in MAOA, OXTR, and AVPR1a and cooperative strategies*" y el segundo titulado "*Effects of experience with access regimes on stewardship behaviors of small-scale fishers*". El primer estudio explora las bases genéticas de estrategias cooperativas. Para ello se evalúa la asociación que existe entre estrategias cooperativas expresadas en un juego de bien público y tres variantes genéticas en una muestra de estudiantes universitarios. El segundo estudio explora el rol de instituciones formales en promover normas de cooperación en grupos de usuarios de recursos naturales. Con esta finalidad se compara la conducta cooperativa de pescadores artesanales en un juego de recurso común contextualizado bajo dos escenarios que recrean dos regímenes de acceso que gobiernan las pesquerías que estos pescadores enfrentan en la vida real. Las diferencias conductuales observadas en el juego entre ambos escenarios son sugestivas de las normas y creencias que los sujetos han internalizado a partir de su experiencia con cada régimen de acceso en la vida real.

II. ABSTRACT

This dissertation explores biological and institutional factors determining human cooperation using an experimental economics approach. It includes two published articles. The first one is called "*No association between genetic variants in MAOA, OXTR, and AVPR1a and cooperative strategies*" and the second one is named "*Effects of experience with access regimes on stewardship behaviors of small-scale fishers*". The first study explores the genetic basis of cooperative strategies in humans. To do so it assesses the association between the strategies displayed by university students in a public good game with the variability observed in three candidate genetic variants. The latter study explores the role played by formal institutions in fostering cooperative norms in groups of users of natural resources. To do this it compares the cooperative behaviors displayed by artisanal fishers in a common pool resource game framed under two scenarios. Each scenario recreates one of two access regimes these fishers face in their real life. The differences in behavior displayed between the two scenarios are suggestive of the norms and expectations that subjects have internalized under each access regime in real life.

III. INTRODUCTION

Cooperation in social dilemmas is key for the success of human societies (Fehr & Fischbacher, 2003). In social dilemmas, self-interest is unaligned with social efficiency (Dawes, 1980; Olson, 1965). Cooperation involves decisions that require the bearing of individual costs in the pursuit of collective benefits. Although cooperation is a ubiquitous phenomenon in humans, variation in cooperative behaviors has been widely documented. Cooperative behaviors differ not only across populations (Balliet & Van Lange, 2013; Henrich et al., 2001; Herrmann et al., 2008; Lamba & Mace, 2011), but also across situations for the same population (Bouma & Ansink, 2013; Dufwenberg et al., 2011; Liberman et al., 2004).

Variability in cooperation has been explained by both biological and social factors. Cumulative evidence suggests a role for neurological structures, hormones, and genes in shaping cooperative behaviors (Ebstein et al., 2010; Kasper et al., 2017). Standards of behavior that apply to specific groups and contexts (i.e., social norms) also affect cooperation by shaping people's expectations and motivations (Ellingsen et al., 2012; Gächter et al., 2010; Goerg & Walkowitz, 2010). Cooperation is key to solve some of the issues most pressing for humanity including climate change and natural resources overexploitation (Ostrom, 1990; Ostrom et al., 1999). Uncovering the biological and social drivers of cooperation can inform the design of effective institutions to promote collective action at the local and global scales.

A major challenge in the study of cooperation is to measure cooperative behaviors in a systematic and unbiased manner. Experimental economics provides a platform to study cooperation under controlled environments, allowing to isolate the effects of different factors on cooperation (Ostrom, 2006). In economic experiments, cooperation is operationalized through the decisions that subjects make in tasks. These tasks are designed based on game theory. Decisions are attached to material payoffs, usually, money, to provide control over subjects' preferences (V. Smith, 1982; V. L. Smith, 1976).

Two decision tasks often used to study cooperation in groups are the public good game and the common pool resource game. The first requires subjects to decide on individual contributions to a public project that brings positive externalities to others. The latter, on the contrary, involves a negative externality that gets materialized when an individual decide to extract units from a common pool. Standard rational theory predicts that people will free ride in both problems (Hardin, 1986). Nonetheless, behaviors displayed in this tasks are heterogenous and often deviate from free riding (Fehr & Schurtenberger, 2018). The ability to capture this diversity in a systematic and controlled manner makes experimental economics a crucial tool to uncover the biological and social mechanisms underlying cooperation. This dissertation uses experimental economics to explore biological and social foundations of human cooperation.

The first study, called “*No association between genetic variants in MAOA, OXTR, and AVPR1a and cooperative strategies*”, assesses to what extent genetic variability accounts for differences in cooperative strategies displayed in a public good game. This work combines behavioral and genetic data from 188 undergraduate students to test the association between cooperative strategies and variability in three genetic variants thought to influence sociality in humans — *MAOA*-uVNTR, *OXTR* rs53576, and *AVPR1* RS3.

The results from previous association studies linking genetic variants with cooperative actions are not robust (Duncan & Keller, 2011; Hewitt, 2012). This lack of robustness is often attributed to low statistical power. Alternatively, it could be due to a confounded measurement of cooperative phenotypes. To explore this latter possibility, this study characterizes cooperative phenotypes based on strategies rather than actions. Unlike actions, strategies do not involve expectations providing a less confounded measurement of cooperative phenotype (Fischbacher et al., 2001; Selten, 1967). To systematically characterize subjects’ strategies, this research uses a public good game in its strategic version (Fischbacher et al., 2001). The results show no evidence of association between cooperative strategies and the genetic variants. These results suggest that refining the characterization of cooperative phenotypes as strategies is not enough to overcome the low power of association studies linking candidate genetic variants with cooperative behaviors.

The second study presented here is called "*Effects of experience with access regimes on stewardship behaviors of small-scale fishers*". It investigates the role of formal institutions in shaping cooperative norms in groups of users of natural resources. The study uses behavioral data of 120 fishers that face two types of access regimes in their real-life fishing activities — collective exclusive access and *de facto* open access.

Fishers played a common pool resource game framed either as the fishing of loco, which is harvested under collective exclusive access or as the fishing of hake, which operates as a *de facto* open access. The results show that fishing communities that have shown high cooperation under collective exclusive access, in real life, displayed higher cooperation in the loco game than in the hake game. There were no differences between frames for communities that have presented relatively low signs of cooperation under collective exclusive access in real life. The observed framing effects in the game are suggestive of the context-specific norms that each group of users holds under each access regime in the real world. These results provide experimental support to the role of collective exclusive access policies in promoting cooperation among users. Yet, they highlight that these formal regimes alone cannot guarantee the internalization of cooperative behaviors.

IV. CITED LITERATURE

Balliet, D., & Van Lange, P. A. M. (2013). Trust, Punishment, and Cooperation Across 18 Societies: A Meta-Analysis. *Perspectives on Psychological Science*, *8*(4), 363–379. https://doi.org/10.1177/1745691613488533

Bouma, J., & Ansink, E. (2013). The role of legitimacy perceptions in self-restricted resource use: A framed field experiment. *Forest Policy and Economics*, *37*(Supplement C), 84–93. https://doi.org/10.1016/j.forpol.2013.01.006

Dawes, R. M. (1980). Social Dilemmas. *Annual Review of Psychology*, *31*(1), 169–193. https://doi.org/10.1146/annurev.ps.31.020180.001125

Dufwenberg, M., Gächter, S., & Hennig-Schmidt, H. (2011). The framing of games and the psychology of play. *Games and Economic Behavior*, *73*(2), 459–478. https://doi.org/10.1016/j.geb.2011.02.003

Duncan, L. E., & Keller, M. C. (2011). A critical review of the first 10 years of candidate gene-by-environment interaction research in psychiatry. *The American Journal of Psychiatry*, *168*(10), 1041–1049. https://doi.org/10.1176/appi.ajp.2011.11020191

Ebstein, R. P., Israel, S., Chew, S. H., Zhong, S., & Knafo, A. (2010). Genetics of Human Social Behavior. *Neuron*, *65*(6), 831–844. https://doi.org/10.1016/j.neuron.2010.02.020

Ellingsen, T., Johannesson, M., Mollerstrom, J., & Munkhammar, S. (2012). Social framing effects: Preferences or beliefs? *Games and Economic Behavior*, *76*(1), 117–130. https://doi.org/10.1016/j.geb.2012.05.007

Fehr, E., & Fischbacher, U. (2003). The nature of human altruism. *Nature*, *425*(6960), 785–791.

Fehr, E., & Schurtenberger, I. (2018). Normative foundations of human cooperation. *Nature Human Behaviour*, *2*(7), 458–468. https://doi.org/10.1038/s41562-018-0385-5

Fischbacher, U., Gächter, S., & Fehr, E. (2001). Are people conditionally cooperative? Evidence from a public goods experiment. *Economics Letters*, *71*(3), 397–404. https://doi.org/10.1016/S0165-1765(01)00394-9

Gächter, S., Herrmann, B., & Thöni, C. (2010). Culture and cooperation. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *365*(1553), 2651–2661. https://doi.org/10.1098/rstb.2010.0135

Goerg, S. J., & Walkowitz, G. (2010). On the prevalence of framing effects across subject-pools in a two-person cooperation game. *Journal of Economic Psychology*, *31*(6), 849–859. https://doi.org/10.1016/j.joep.2010.06.001

Hardin, G. (1986). The Tragedy of the Commons. *Science*, *162*(3859), 1243–1248.

Henrich, J., Boyd, R., Bowles, S., Camerer, C., Fehr, E., Gintis, H., & McElreath, R. (2001). In Search of Homo Economicus: Behavioral Experiments in 15 Small-Scale Societies. *The American Economic Review*, *91*(2), 73–78.

Herrmann, B., Thöni, C., & Gächter, S. (2008). Antisocial Punishment Across Societies. *Science*, *319*(5868), 1362–1367. https://doi.org/10.1126/science.1153808

Hewitt, J. K. (2012). Editorial policy on candidate gene association and candidate gene-by-environment interaction studies of complex traits. *Behavior Genetics*, *42*(1), 1–2. https://doi.org/10.1007/s10519-011-9504-z

Kasper, C., Vierbuchen, M., Ernst, U., Fischer, S., Radersma, R., Raulo, A., Cunha-Saraiva, F., Wu, M., Mobley, K. B., & Taborsky, B. (2017). Genetics and developmental biology of cooperation. *Molecular Ecology*, *26*(17), 4364–4377. https://doi.org/10.1111/mec.14208

Lamba, S., & Mace, R. (2011). Demography and ecology drive variation in cooperation across human populations. *Proceedings of the National Academy of Sciences*, *108*(35), 14426–14430. https://doi.org/10.1073/pnas.1105186108

Liberman, V., Samuels, S. M., & Ross, L. (2004). The Name of the Game: Predictive Power of Reputations versus Situational Labels in Determining

Prisoner's Dilemma Game Moves. *Personality and Social Psychology Bulletin*, *30*(9), 1175–1185. https://doi.org/10.1177/0146167204264004

Olson, M. (1965). *The logic of collective action*. Harvard University Press.

Ostrom, E. (1990). *Governing the commons: The evolution of institutions for collective action*. Cambridge University Press.

Ostrom, E. (2006). The value-added of laboratory experiments for the study of institutions and common-pool resources. *Journal of Economic Behavior & Organization*, *61*(2), 149–163. https://doi.org/10.1016/j.jebo.2005.02.008

Ostrom, E., Burger, J., Field, C. B., Norgaard, R. B., & Policansky, D. (1999). Revisiting the Commons: Local Lessons, Global Challenges. *Science*, *284*(5412), 278–282. https://doi.org/10.1126/science.284.5412.278

Selten, R. (1967). Die Strategiemethode zur Erforschung des eingeschrankt rationalen Verhaltens im Rahmen eines Oligopolexperimentes. In H. Sauermann (Ed.), *Beitrage zur experimentellen Wirtschaftsforschung* (pp. 136–168). J.C.B. Mohr (Paul ¨ Siebeck).

Smith, V. (1982). Microeconomic Systems as an Experimental Science. *The American Economic Review*, *72*(5), 923–955.

Smith, V. L. (1976). Experimental Economics: Induced Value Theory. *The American Economic Review*, *66*(2), 274–279.

V. APPENDIX

PLOS ONE

RESEARCH ARTICLE

No association between genetic variants in *MAOA*, *OXTR*, and *AVPR1a* and cooperative strategies

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Abstract

The effort to understand the genetic basis of human sociality has been encouraged by the diversity and heritability of social traits like cooperation. This task has remained elusive largely because most studies of sociality and genetics use sample sizes that are often unable to detect the small effects that single genes may have on complex social behaviors. The lack of robust findings could also be a consequence of a poor characterization of social phenotypes. Here, we explore the latter possibility by testing whether refining measures of cooperative phenotypes can increase the replication of previously reported associations between genetic variants and cooperation in small samples. Unlike most previous studies of sociality and genetics, we characterize cooperative phenotypes based on strategies rather than actions. Measuring strategies help differentiate between similar actions with different underlaying social motivations while controlling for expectations and learning. In an admixed Latino sample (n = 188), we tested whether cooperative strategies were associated with three genetic variants thought to influence sociality in humans—*MAOA*-uVNTR, *OXTR* rs53576, and *AVPR1* RS3. We found no association between cooperative strategies and any of the candidate genetic variants. Since we were unable to replicate previous observations our results suggest that refining measurements of cooperative phenotypes as strategies is not enough to overcome the inherent statistical power problem of candidate gene studies.

Introduction

The questions of why and when people are willing to cooperate, bearing individual costs in the pursuit of collective benefit, have been a major focus in the social and natural sciences [1–4]. Although cooperation is widespread among humans, there is considerable diversity among cooperative behaviors [5–8]. Evidence supporting the heritability of social traits has encouraged efforts to understand the genetics underlying this diversity [9–11]. Although several

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studies have searched for genetic variation associated with cooperation and related behaviors, such as trust, reciprocity, and altruism, this task has remained elusive [3].

The existing literature relies heavily on studies that test the association between social phenotypes and a handful of candidate gene variants using small sample sizes of few hundred individuals (i.e. candidate genes studies) [12, 13]. The results of these studies are inconsistent and usually not replicable [14–17]. The most accepted explanation for the lack of robust findings is that most candidate gene studies lack statistical power given the small effects that single variants may have on complex social traits [14, 18–20]. The lack of robust associations could also be a consequence of a poor characterization of cooperative phenotypes. This possibility, which we aim to address in this study, has largely been overlooked in the literature.

A common approach to characterizing social phenotypes is to measure actions displayed in incentive-based tasks grounded on game-theoretic experimental paradigms (see Table 1 for a summary of this literature). However, actions displayed in these tasks result from the interaction of multiple cognitive processes. For example, in tasks for which the outcome is given by the simultaneous decisions of multiple players, actions are influenced by the expectations of subjects about the behavior of others [21]. Additionally, in tasks involving repeated decisions, actions are influenced by learning [22]. Expectations and learning are likely to involve different neural networks and structures [23]. Therefore, unpacking cooperative traits into more elementary constructs could help elucidate associations with particular genetic variants [24].

Strategies are game-theoretic constructs that can reflect social motivations while controlling for expectations and learning. A strategy is a player's contingent plan specifying her/his actions in response to all the possible actions of the other players. The standard prediction in economics is that, in contexts that require cooperation, individuals will choose to free-ride no matter what others do. However, strategies in cooperative contexts are diverse and the "free-riding" strategy is not the most prevalent [5, 6, 8]. Most people condition their cooperation on their counterparts' behaviors. The majority chooses to closely match the levels of cooperation of their counterparts, a strategy that is usually referred to as "conditional cooperation"[2]. Some individuals prefer to match the levels of cooperation of their counterparts only up to a certain level at which they start decreasing their contributions, a strategy that is referred to as "hump-shaped" [5]. In situations where the actions of others are unknown, those that like to condition their actions on what others do will behave based on their expectations about the decisions of others [2]. Therefore, if only actions are observed, as is the case in most candidate gene studies, it is not possible to discriminate between conditional cooperation, hump-shaped, and free-riding strategies. This differentiation is possible, however, if incentive-based tasks are designed to elicit strategies rather than actions. Specifically, to use the "strategy-method" [25] rather than the standard direct response method allows identifying underlying strategies in the context of a public goods game (PGG), a task widely used to study cooperation [5].

Recent evidence supports the inheritability of cooperative strategies [11] and sheds light on its neurological basis [26]. To our knowledge, only Mertins et al. [27] have reported association of a genetic variant with cooperative strategies, *MAOA*-uVNTR, located in the gene that codes for monoamine oxidase A, which metabolizes monoamine neurotransmitters. Variants in this gene lead to a lower expression (MAOA-L) or higher expression (MAOA-H) of monoamine oxidase A [28]. Mertins et al. [27] found that women with MAOA-L variants are less likely to behave like free-riders than MAOA-H carriers. Similarly, it has been observed that women carrying MAOA-L variants cooperate more in repeated interactions [29] and that MAOA-L genotypes correlate with social sensitivity [30].

Other variants that have been associated with social behaviors are in genes that encode receptors for oxytocin and vasopressin, two neurotransmitters highly linked to sociality [31]. The single nucleotide variant rs53576 in *OXTR* and the microsatellite RS3 in *AVPR1a* have

Table 1. Summary of previous studies of genetics and sociality using incentive-based tasks.

Reference	Sample size	Population	Incentive-based task	Involves expectations (i.e. simultaneous decisions)	Involves learning (i.e. repeated decisions)	Social trait	Candidate gene	Result
Knafao et al., 2008 [37]	203 (101 women)	College students from Israel	Dictator game	No	No	Altruism	*AVPR1A*	Carriers pf shorter variants of the *AVPR1a* RS3 repeat showed less altruistic behavior than carriers of longer variants.
Israel et al., 2009 (first sample) [75]	203 (102 women)	College students from Israel and their families	Dictator game	No	No	Altruism	*OXTR*	Variants of rs1042778, rs237887, and rs2268490 were association with altruism.
Israel et al., 2009 (second sample) [75]	98 (all women)	Mothers from Israel	Dictator game	No	No	Altruism	*OXTR*	Variants of rs1042778, rs237887, and rs2268490 were association with altruism.
Apicella et al., 2010 [67]	684 (80% women)	Swedish twins	Dictator game	No	No	Altruism	*OXTR*	No association
			Trust game with trustee role in strategy method	Yes, for the trustor	No	Trust and trustworthiness		
Zhong et al., 2010 [76]	208 (54% women)	Chinese Han	Ultimatum game	Yes	No	Fairness	*DRD4*	DRD4 is associated with fairness preference
Avinun et al., 2011 [43]	158 (81 women)	Israeli preschool twins	Dictator game	No	No	Altruism	*AVPR1A*	Carriers of the variant with 327 bp showed lower altruism compared to other subjects
Mertins et al., 2011 [29]	96 (60 women)	Students at the University of Trier in Germany	Repeated public good game	Yes	Yes	Cooperation	*MAOA*	Men carriers of the low activity alleles cooperate significantly less than those carrying the high activity alleles
Krueger et al., 2012 [66]	108 (all men)	College students with European ancestry	Trust game	Yes	Yes	Trust and trustworthiness	*OXTR*	GG genotype for rs53576 showed higher trust than AA and AG genotypes
Chew et al., 2013 (first sample) [77]	208 (112 women)	Han Chinese	Ultimatum game	Yes	No	Fairness	*AR*, *ERα*, and *ERβ*	*AR* associated with minimal acceptable offers in men. *Erβ* associated with minimal acceptable offers in women.
Chew et al., 2013 (second sample) [77]	257 (125 women)	Israeli	Ultimatum game	Yes	No	Fairness	*AR*, *ERα*, and *ERβ*	*Erβ* marginally associated with minimal acceptable offers in women.
Mertins et al., 2013 [27]	91 (58 women)	Students at the University of Trier in Germany	Public good game using strategy method	No	No	Cooperation	*MAOA*	Women carriers of the low activity alleles were less likely to behave as weak free riders compared to women carrying high activity alleles
Reuter et al., 2013 [78]	130 (105 women)	Caucasians	Ultimatum game	Yes	No	Fairness	*DRD2* and *DRD4*	4/4 genotype for the *DRD4* variant showed a higher minimal acceptable offer than other genotypes
Schroeder et al., 2013 [79]	184 (107 women)	Students at Newcastle University in England	Repeated Public good game	Yes	Yes	Cooperation	*SLC6A4* and *HTR2A*	*SLC6A4* was associated with cooperation in the absence of punishment. In the presence of punishment, cooperation was associated with *HTR2A*
Feng et al., 2015 [36]	204 (100 women)	Students at the Emory University in the United States of America	Iterated sequential Prisoner's Dilemma Game	No	Yes	Cooperation	*OXTR*	Sex differences in effects of intranasal oxytocin treatment for individuals with the GG genotype

(*Continued*)

Table 1. (Continued)

Reference	Sample size	Population	Incentive-based task	Involves expectations (i.e. simultaneous decisions)	Involves learning (i.e. repeated decisions)	Social trait	Candidate gene	Result
Nishina et al., 2015 [35]	470 (242 women)	Non-student Japanese	Trust game with trustee role in strategy method	Yes, for the trustor	No	Trust and trustworthiness	*OXTR*	GG genotype for *OXTR* rs53576 showed higher trust than AA genotype in men
Wang et al., 2016 [38]	278 (150 women)	Chinese Han	Dictator game	No	No	Altruism	*AVPR1A*	Men with relatively short variants of RS3 allocated less money to others compared with men carrying two copies of long variants
Nishina et al., 2019 [39]	434 (221 women)	Non-student Japanese	Trust game with trustee role in strategy method	Yes, for the trustor	No	Trust and trustworthiness	*AVPR1a*	Men with a short form of *AVPR1a* showed more trust than those carrying other variants. Additionally, subjects with a short form of *AVPR1a* displayed higher trustworthiness

Summary of the design features of candidate gene association studies using incentive-based tasks to measure social traits.

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emerged as promising candidates for social behavior. Individuals homozygous for the G allele (GG) of *OXTR* rs53576 show higher levels of empathy [32], sociality [33, 34], and higher levels of trust [35] compared to individuals with one or two copies of the A allele (AA/AG). It has also been suggested that the G allele modulates the effect of oxytocin in cooperative interactions [36]. The lengths of variants of *AVPR1a* RS3 also correlate with cooperation-related social traits. For instance, individuals with relatively long repeats in *AVPR1a* RS3 are more altruistic [37, 38], but are less trusting and disposed to reciprocity [39].

We aim to explore whether more refined measures of cooperative phenotypes—underlying strategies rather than observable actions—support the replicability and robustness of previously reported associations. We replicate the analysis of Mertins et al. [27], by testing the association between cooperative strategies and *MAOA*-uVNTR variants in an admixed Latino population and extended it by including *OXTR* rs53576, and *AVPR1a* RS3 as additional candidates (n = 188).

Methods

Subjects and recruitment

Our sample consisted of 200 Chilean students (18 to 25 years old, women = 109) from Universidad del Desarrollo (UDD), in Santiago, Chile. Subjects were recruited two weeks prior to the experimental sessions by emailing all students an invitation to participate in a study about genetics and decision-making and recruitment posters were distributed on campus. Volunteers filled out an online form with their contact information and availability. The only inclusion criterion was that subjects be students at UDD at the time of participation.

Experimental procedures

We conducted 10 sessions in a computer laboratory at UDD between June and September 2013. Subjects were notified of an experimental session via email and were offered a show-up fee of $2.500 CLP, plus additional earnings from the incentive-based task. In each session, 20 students entered the room and were seated in front of an individual computer. The facilitator informed the subjects that their participation would consist of playing a four-person PGG, after which they would provide a saliva sample. Subjects were also informed that decisions would be recorded anonymously and that they could leave the experiment at any moment. The game was programmed in z-Tree [40] and communication during the game was not allowed. A printed copy of the instructions of the game was handed to each participant and the facilitator read them aloud at the beginning of the session (S1 Text). Examples of outcomes were shown, and questions were answered aloud before the game started. Our protocol was approved by the UDD Research Ethics Committee.

Each individual in the game was given 20 tokens (valued $250 CLP) and had to privately decide how many tokens to contribute to the public good and how many to keep for themselves. Contributions to the public goods were doubled and divided into equal parts among the four members in the group, regardless of how many each member contributed. The game's payoff function was:

$$\pi_i = (20 - g_i + 0.5\sum_{j=1}^{j=4} g_j) \times \$250\ CLP$$

Where π_i is the final payoff of subject i, $g_i \in \{0,1,\ldots,20\}$ is the contribution of individual i to the public goods, and $g_j \in \{0,1,\ldots,20\}$ is the contribution of each member of the group. As the marginal gain of contributing one token to the public good is 0.5 while the marginal gain of keeping it is one, we expected no contributions to the public good under the assumption of self-interested, profit-maximizing individuals.

We used the PGG game protocol developed by Fischbacher et al. [5] in which subjects are asked to make two types of decisions: an "uninformed contribution" and a "contingent contribution". The uninformed contribution was the answer to the question: You have 20 tokens; how many tokens will you contribute to the public goods? (S1 Fig). This question did not provide subjects with information about what other members of the group were contributing. Consequently, this decision involved individual expectations about the contributions of others. The contingent contribution required that subjects answer the question of how many of their 20 tokens they would contribute to the public goods given a scenario in which the other members of the group contribute an average of $\bar{g}_{j\neq i}$ tokens (rounded to the integer), with $\bar{g}_{j\neq i} \in \{0,1,2\ldots20\}$ (S2 Fig). The answer to this question elicited cooperative strategies which exclude the confounding effects of intertemporal strategies, learning or expectations about the cooperative behavior of others.

After subjects provided their answers for their uninformed and contingent contributions, they were randomly and anonymously matched by the software into groups of four. The uninformed contributions of three random players in the group were averaged and rounded to the integer to obtain $\bar{g}_{j\neq i}$, which was then employed to find the contribution of the fourth player based on her/his contingent contribution. This provided the total contribution to the public goods, and individual payoffs were calculated. This procedure ensured that both answers were incentive compatible as both could be considered to calculate individual payoffs.

Saliva samples were collected at the end of the session using Saliva Self-Collection Kit OG 500 (DNA Genotek, Canada). Each subject provided a sample in a tube labeled with the same identification code under which the subject's answers in the game were recorded. Subjects collected their profits privately in a separate room.

Genotyping

DNA was successfully extracted from 188 samples (women = 107). The three candidate variants were analyzed as described in the protocols of previous studies [41–43]. Results revealed four alleles for *MAOA*-uVNTR in our sample presenting 3.5, 4.5, 5.5, and 6.5 repeats (S1 Table). These alleles correspond respectively to the 3, 4, 5, and 6 repeats alleles observed in previous studies [44]. Given the low frequencies of the 5.5 and 6.5 repeats alleles in our sample, we excluded their carriers from the analysis. Since the *MAOA* gene is in the X chromosome, men only have one allele for *MAOA*-uVNTR, therefore genotypes for men are 4.5 and 3.5 repeats, equivalent to the MAOA-H and MAOA-L, respectively [28]. In the case of women, one of the two X chromosomes in somatic cells becomes transcriptionally inactive early in development [45]. We cannot determine which of the alleles is being expressed in women that are heterozygous for *MAOA*-uVNTR, therefore we excluded them from the analysis. This left us with the two homozygous genotypes of *MAOA*-uVNTR in women—4.5/4.5 and 3.5/3.5 repeats—equivalent to the MAOA-H and MAOA-L variants, respectively [28]. Consequently, genotypes for *MAOA* u-VNTR were coded under "MAOA-H" or "MAOA-L" in both women and men.

Genotypes for *OXTR* rs53576 were coded as "GG", "GA", and "AA". Alleles for *AVPR1a* RS3 were classified as "Short" if they were between 324 bp to 341 bp long and as "Long" if they were between 342 bp to 356 bp long (S2 Table). This cutoff was established to ensure that both groups were balanced in the number of observations. This classification method is often used for microsatellite repeats due to a usually high number of low-frequency alleles [37]. Genotypes for the RS3 *AVPR1a* were coded as "Short/Short", "Short/Long" and "Long/Long".

The resulting genotype distribution satisfies Hardy-Weinberg equilibrium for *AVPR1a* RS3 ($X^2 = 2.84$, $p = 0.09$) and *MAOA* u-VNTR ($X^2 = 0.18$, $p = 0.67$, tested only for women because it is a sex-linked variant), but not for *OXTR* rs53576 ($X^2 = 5.29$, $p = 0.02$) (S3 and S4 Tables show genotype distributions for women and men).

Identification of cooperative strategies

We classified each subject's cooperative strategy into four types using the following classification algorithm. First, subjects whose maximum contribution in the contingent contribution table was below or equal to 20% of the endowment (4 tokens) were considered as free riders (FR). For strategies that did not enter the FR category, we proceeded as follows; for each strategy we ran two simultaneous Spearman rank correlations between the subject's contingent contribution and others' hypothetical average contribution. Initially, the first correlation considered the first three entries in the contingent contribution table (when others' hypothetical average contribution was 0, 1, and 2) and the second correlation considered the rest of the entries in the contingent contribution table (when others' hypothetical average contribution was 3, 4, . . ., 20). We repeated this procedure for each strategy by including each entry sequentially in the first correlation and removing it from the second correlation until the first correlation considered the first 18 entries in the contingent contribution table (when others' hypothetical average contribution was 0, 1, . . ., 17) and the second correlation considered the last three entries in the contingent contribution table (when others' hypothetical average contribution was 18, 19, 20). Strategies were classified as hump-shaped (HS) if they showed at least one positive-to-negative change between the first and second correlation in the sign of their Spearman correlation coefficient at a 1% significance level. The remaining strategies were classified as conditional cooperators (CC) if they displayed a significantly positive Spearman coefficient (at a 1% significance level). Following Fischbacher et al. [5], we classified all the strategies that did not fall into FR, HS, or CC as others (OT). The OT category consists of strategies that presented miscellaneous patterns of contributions, including unconditional cooperation (three players) (see S3 Fig for individual OT strategies). We ran robustness checks with different FR classification criteria which considered subjects whose maximum contribution in the contingent contribution table was below or equal to 10% and 30% of the endowment.

Statistical analysis

We ran all our analysis separately for each sex since previous studies suggest sex-specific associations [e.g. 27, 39]. We applied Bonferroni correction to account for multiple hypotheses testing in each set of analyses. Associations between genetic variants and cooperative strategies were tested using a Fisher exact test ($\alpha = 0.008$ given six hypotheses). Additionally, to test the relationship between specific genotypes and cooperative strategies we ran a multinomial logistic regression model with bootstrapped standard errors for each variant. Then, we calculated the marginal effects of each genotype on the probability of a subject displaying a given cooperative strategy ($\alpha = 0.00125$ given 40 hypotheses).

Following Mertins et al. [27], we also tested whether mean contingent contributions differed between genotypes under three cooperative scenarios. The "low contribution scenario" is the first seven entries in the contingent contribution table (i.e. when the mean hypothetical others' contribution goes from 0 to 6 tokens), the "mid contribution scenario" is the next seven entries in the table (i.e. when the mean hypothetical others' contribution goes from 7 to 13 tokens), and the "high contribution scenario" is the last seven entries in the table (i.e. when the mean hypothetical others' contribution goes from 14 to 20 tokens). We ran Kruskal-Wallis rank tests to test significant differences in mean contribution between genotypes for each variant under the three scenarios ($\alpha = 0.003$ given 18 hypotheses) ant to test whether uninformed contributions significantly differed between genotypes for each variant ($\alpha = 0.008$ given six hypotheses). All analyses were run in R Studio v1.1.456 except multinomial logistic regressions which were run in Stata v.12.0. Data and code are available at https://github.com/ignacia-rivera/genetics_coop.

Results

The distribution of cooperative strategies is presented in Table 2. No significant difference was observed in the distribution of cooperative strategies of women and men ($p = 0.545$, two-sided Fisher test). The average profile for each type of strategy is shown in Fig 1. The average CC strategy deviates from the diagonal (perfect conditional cooperation) downwards displaying a bias towards selfishness.

The distribution of cooperative strategies for each genotype is shown in Fig 2. No association between cooperative strategies and any of the variants was found, either for women or men ($p \geq 0.145$, two-sided Fisher exact test). This result holds for classification criteria that use a cutoff of 10 and 30% of the endowment to characterize the FR strategy. Our regression analysis confirmed this result since no genotype was found to have a significant effect on the probability of a subject displaying a particular type of strategy after correcting for multiple hypotheses testing ($p \geq 0.01$ with $\alpha = 0.00125$, dy/dx from multinomial logistic regression, S5 and S6 Tables).

Table 2. Percentage distribution of cooperative strategies.

Cooperative strategy	Percentage of women (%)	Percentage of men (%)
CC	44.86	54.32
HS	12.15	11.11
FR	9.35	9.88
OT	33.64	24.69

Percentage distribution of cooperative strategies for women (n = 107) and men (n = 81). Considering as a FR any strategy in which the maximum contingent contribution was equal or below 20% of the endowment.

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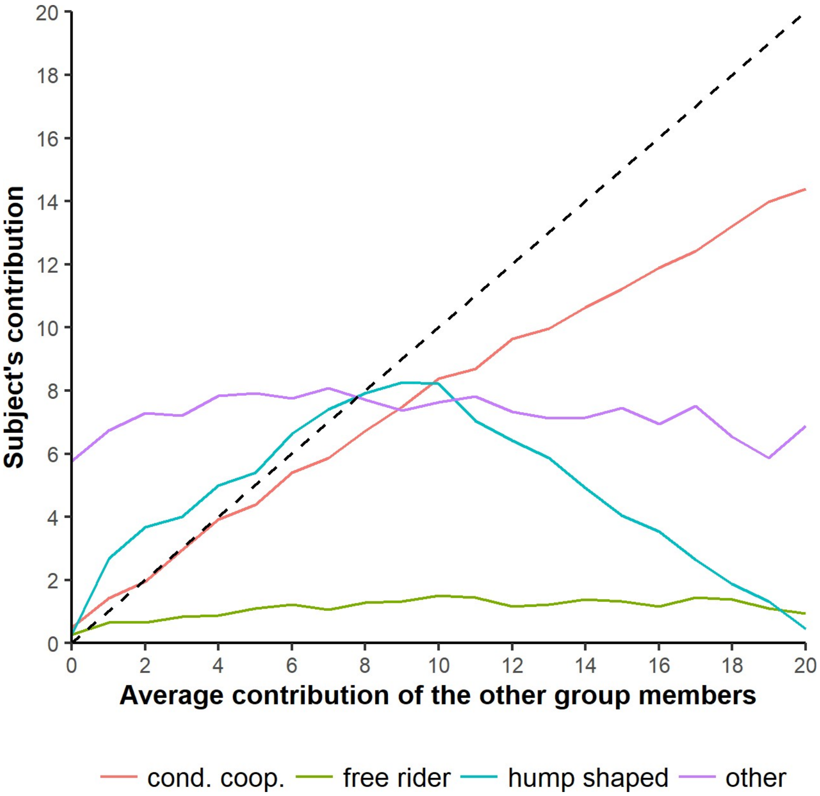

Fig 1. Average profile for each type of strategy. Average cooperative strategy for free riders (green), conditional cooperators (red), hump shaped (light blue) and others (purple). Dashed line represents the contribution profile of a perfect conditional cooperator.

https://doi.org/10.1371/journal.pone.0244189.g001

Some patterns could be distinguished between genotypes in their average strategy (Fig 3). For *OXTR* rs53756, AA women tended to contribute more than other genotypes when the average contribution of others was between around six and 14 tokens, while AA men seemed to contribute less than other genotypes when the average contribution of others was below 10 tokes. Women carrying Long and Short copies for *AVPR1a* RS3 reduced their levels of contribution once the average contribution of others reached approximately nine tokens relative to the homozygous types. Among men, Long/Long genotypes of *AVPR1a* RS3 presented strategies with generally lower contributions compared to the strategies of Short alleles carriers. MAOA-L women displayed strategies with higher contributions relative to MAOA-H women when the average contribution of others was less than approximately 6 tokens. In the case of men, MAOA-L showed higher contribution levels than MAOA-H when the average contribution of others was higher than 10 tokes. Despite these observed patterns, we found no statistically significant differences between genotypes regarding their mean contingent contribution under different cooperative scenarios (i.e. “high contribution”, “mid contribution” and “low contribution” scenarios) ($p \geq 0.025$ with $\alpha = 0.003$, Kruskal-Wallis rank test). No significant differences in uninformed contributions were found between genotypes for any of the variants neither for women nor men ($p \geq 0.18$, Kruskal-Wallis).

Discussion

Unlike most candidate gene studies that investigate associations with observable actions, we tested whether candidate variants are associated with underlying strategies. Our results showed

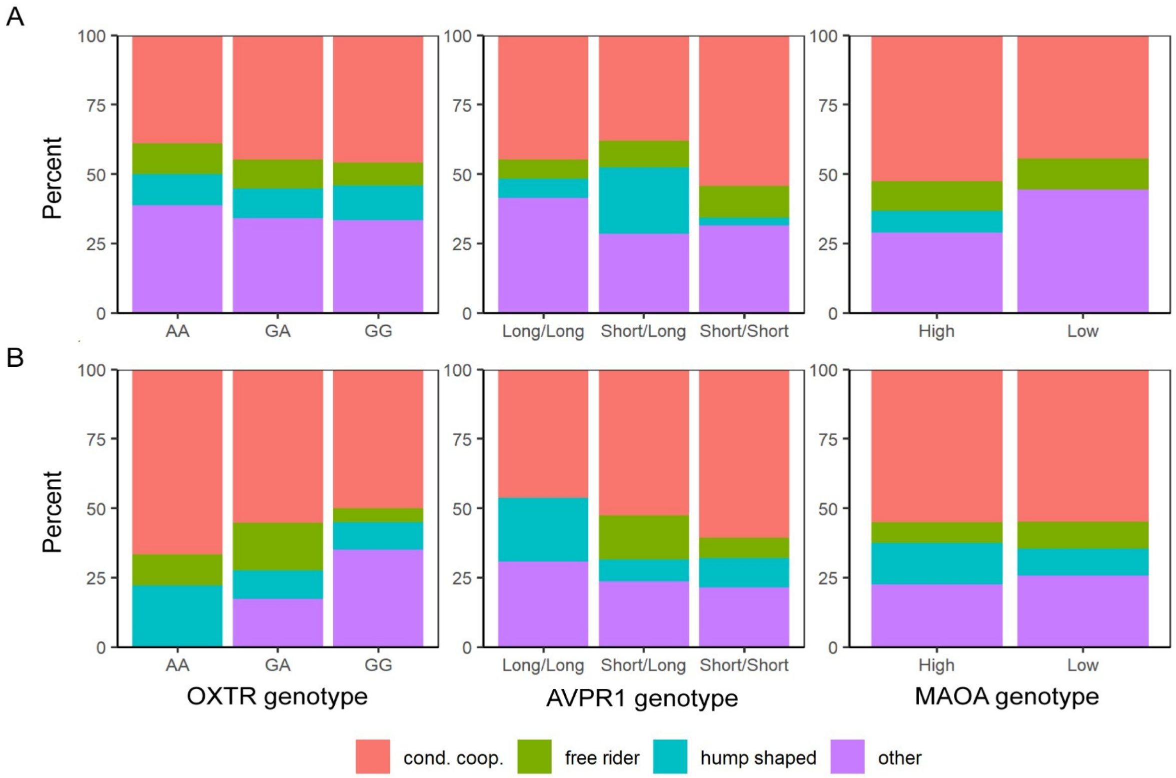

Fig 2. Distribution of cooperative strategies for each genotype. Percentage distribution of cooperative strategies, conditional cooperators (red), hump shaped (light blue), free riders (green) and others (purple) for AA (n = 18), GA (n = 38), and GG (n = 48) *OXTR* rs53576 genotypes; for Long/Long (n = 29), Short/Long (n = 42), and Short/Short (n = 35) *AVPR1a* RS3 genotypes; High (n = 9) and Low (n = 38) *MAOA* u-VNTR genotypes in women (panel A). Percentage distribution of cooperative strategies for AA (n = 9), GA (n = 29), and GG (n = 40) *OXTR* rs53576 genotypes; for Long/Long (n = 13), Short/Long (n = 38), and Short/Short (n = 28) *AVPR1a* RS3 genotypes; High (n = 31) and Low (n = 40) *MAOA* u-VNTR genotypes in men (panel B).

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no association between cooperative strategies and the three studied variants: *MAOA*-uVNTR, *OXTR* rs53576, and *AVPR1 RS3*. Therefore, our findings did not replicate previous results by Mertins et al. [27] for *MAOA*-uVNTR and did not match expected associations based on previous results linking *OXTR* rs53576, and *AVPR1* RS3 with sociality. This suggests that when cooperative phenotypes are measured more precisely as strategies—which exclude learning and expectations—associations with candidate genetic variants cannot be consistently replicated in small samples. This is in line with the consensus amongst geneticists that no single gene can explain a meaningful part of the variance observed in humans social traits [14, 15, 17–20, 46].

We characterize a cooperative phenotype as the subjects' strategies in a PGG using the protocol by Fischbacher et al. [5]. The results from applying this method have been replicated in samples around the world, showing that the most prevalent strategy is CC [8]. To our knowledge, we report the first application of this protocol to elicit cooperative strategies in an admixed Latino sample. We replicated the main finding that the most frequent strategy is CC in both women and men, with frequencies that fall within the range of previous studies (from around 40% to 70% of trials) [8]. Typically, studies find that the second most frequent strategy is FR. In our sample, however, the second most frequent strategy was HS. Nonetheless, the frequencies we found for both HS and FR fall within the ranges observed in previous studies [8]. We found a high number of strategies that could not be categorized within the CC, FR, or HS

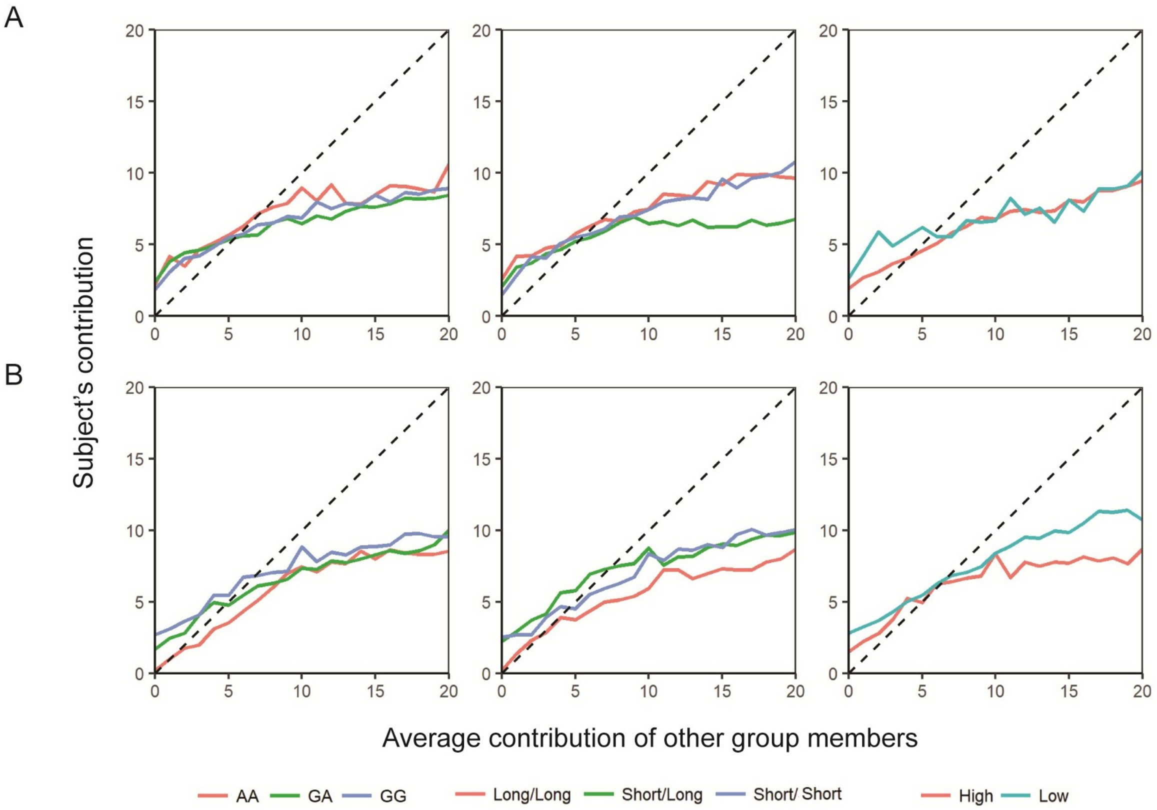

Fig 3. Average cooperative strategies per genotype. Average cooperative strategies per genotype for *OXTR* rs53576, *AVPR1a* RS3, and *MAOA* u-VNTR in women (panel A) and in men (panel B).

https://doi.org/10.1371/journal.pone.0244189.g003

categories (i.e. around 34% for women and 24% for men), which we classified as OT. The share of OT observed in our sample is high compared to what has been observed in most studies, but still within the ranges reported by other researchers [47]. The high number of OT in our sample relative to other studies can be due to differences in classification criteria as well as in populations. Overall, our behavioral results replicate broader strategy patterns found in previous studies and therefore provide a robust characterization of the cooperative inclinations defined in the experimental economics literature.

The strategy method purposely minimizes the effect that others have on individual decisions to elicit a controlled measure of cooperative preferences. Yet, cooperative interactions also involve social cognitive processes such as emotion recognition [48, 49], empathy and theory of mind [50], social communication [51], and social reward seeking [52]. All of those are excluded from our measurement of cooperation and could be influenced by the genetic variants studied here. Indeed, a study by [29] suggests that variation in *MAOA-uVNTR* correlates with differences in expectations about others' behaviors, and variations in *OXTR* have been associated with empathy [53] and social reward [12, 54]. Furthermore, it has been suggested that empathy and perspective taking mediate the effects of *OXTR* on prosocial behavior [55]. This highlights the importance of disentangling the multiple cognitive phenomena involved in complex behaviors such as cooperation when aiming to link them to variation in candidate genes.

At least, three reasons can explain the lack of replicability and mismatch with previous related observations. First, our admixed Latino population differs, both genetically and environmentally, from the Caucasian and Asian populations commonly studied in similar candidate gene studies (see **Table 1**). Variability in associations between populations can arise due to differences in gene-environment interactions [56]. Indeed, it has been suggested that social behaviors are influenced by culture which can mask genetic influences differentially across populations [57]. Different patterns of linkage disequilibrium can also explain differences in gene-trait associations across populations [58].

A second possible reason why we did not find the associations suggested by previous studies is that previous studies may have misrepresented the association between these candidate variants and cooperative traits. Despite having selected our candidate variants based on an exhaustive literature review, new evidence has come to question common findings in this body of research. In particular, there are serious methodological concerns about the validity of several observations linking oxytocin with trust, which is one of the most studied associations in social neuroscience [59–62]. For instance, the association between exogenous intranasal oxytocin and higher levels of trust [54, 63] and the correlation between trust and oxytocin plasma levels [64] has been poorly replicated [60, 65]. Lack of robust results linking trust with *OXTR* has also been evidenced in candidate gene studies. For example, while [66] reported a significant association between *OXTR* rs53576 and investments in a trust game, [67] reported no association in a larger sample (N = 684). Moreover, many results of candidate gene studies are thought to be false positives since most of them do not account for family-wise error [46]. Indeed, if we had not corrected for multiple hypotheses testing, we would have observed significant misleading associations. All this demonstrates the susceptibility of candidate gene studies to fall into biases by following genetic variants overrepresented in the literature and underscores the value of publishing null results.

The third explanation for the lack of associations observed in our study is insufficient statistical power. In theory, more refined measurements of social phenotypes should increase a study's capacity to detect associations between genes and social traits. Nonetheless, our results suggest that refining the characterization of cooperative phenotypes is not enough to overcome the problem of inherently low statistical power of candidate gene studies. This detection problem is fundamentally due to the small effects that single genes have on complex social behaviors, such that they would require massive sample sizes to be detected. Consequently, geneticists seriously question the value of candidate gene studies to understand the underlying genetics of complex social behaviors [14, 17–19].

Successful candidate gene studies would require sufficiently large samples and candidate variants that have a credible high prior probability of being associated with the trait of interest [19, 46]. Therefore, there is still a need to better understand the links between genotype and cooperation using approaches with higher statistical power before implementing promising candidate genes studies. Genome-wide association studies (GWAS) —which simultaneously explore thousands of variants while accounting for family-wise error in a hypothesis generating manner — have a lot to offer in terms of pointing to potentially relevant genetic variants [68–72]. Nonetheless, GWAS that directly explore cooperation are still lacking and those that have looked into similar prosocial constructs have not found significant associations [14, 73]. Studies involving neuroimaging and neurotransmitter measurements are also promising to identify neurobiological pathways involved in cooperative decision making [38, 74]. These studies can further point to promising candidate genes by narrowing down the neural structures, molecules, and networks involved in cooperative decisions.

We explored whether refining the measurement of cooperative phenotypes as strategies rather than actions increases the capacity of a candidate gene study to replicate associations between candidate variants and cooperation in a small sample. Our results suggest that this approach alone cannot solve the inherent statistical power problem of this type of studies.

Nonetheless, the refinement of cognitive constructs in GWAS and their proper measurement is still a promising approach to improve our ability to detect genes associated with complex behaviors. Better measurements can be informed by novel designs developed by behavioral scientists that allow unpacking decisions involving multiple cognitive phenomena like the strategy method implemented in our study.

Supporting information

S1 Text. Game instructions. Instructions of the game presented to the subjects in Spanish.
(DOCX)

S1 Fig. Screen 1. Screen to collect decisions for the "uninformed player" role (text in Spanish).
(DOCX)

S2 Fig. Screen 2. Screen to collect decisions for the "informed player" role (text in Spanish).
(DOCX)

S3 Fig. Individual schedules for strategies categorized as those of others. Each plot shows the strategies of five individuals except the last one which shows six.
(DOCX)

S1 Table. Frequency of *MAOA* u-VNTR alleles.
(DOCX)

S2 Table. Frequency and classification of *AVPR1a* RS3 alleles based on length (number of base pairs).
(DOCX)

S3 Table. Frequency of the genotypes for each variant in women.
(DOCX)

S4 Table. Frequency of the genotypes for each variant in men.
(DOCX)

S5 Table. Marginal effects of each genotype on each cooperative strategy in women. Obtained from a multinomial logistic regression model for each genetic variant that uses cooperative strategy as a dependent variable and genotypes as independent variables. For *OXTR* rs53567 AA is the baseline genotype (n = 104), for *AVPR1* RS3 Long/Long is the baseline genotype (n = 106), and for *MAOA* u-VNTR the Low expression is the baseline genotype (n = 47).
(DOCX)

S6 Table. Marginal effects of each genotype on each cooperative strategy in men. Obtained from a multinomial logistic regression model for each genetic variant that used cooperative strategy as a dependent variable and genotypes as independent variables. For *OXTR* rs53567 AA is the baseline genotype (n = 78), for *AVPR1* RS3 Long/Long is the baseline genotype (n = 79), and for *MAOA* u-VNTR the Low expression is the baseline genotype (n = 71).
(DOCX)

S1 Data.
(CSV)

Author Contributions

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References

1. Barkow JH, Cosmides L, Tooby J. The Adapted Mind: Evolutionary Psychology and the Generation of Culture. Oxford University Press; 1992. PMID: 1551765
2. Fehr E, Schurtenberger I. Normative foundations of human cooperation. Nature Human Behaviour. 2018; 2: 458–468. https://doi.org/10.1038/s41562-018-0385-5 PMID: 31097815
3. Kasper C, Vierbuchen M, Ernst U, Fischer S, Radersma R, Raulo A, et al. Genetics and developmental biology of cooperation. Mol Ecol. 2017; 26: 4364–4377. https://doi.org/10.1111/mec.14208 PMID: 28626971
4. Rand DG, Nowak MA. Human cooperation. Trends in Cognitive Sciences. 2013; 17: 413–425. https://doi.org/10.1016/j.tics.2013.06.003 PMID: 23856025
5. Fischbacher U, Gächter S, Fehr E. Are people conditionally cooperative? Evidence from a public goods experiment. Economics Letters. 2001; 71: 397–404. https://doi.org/10.1016/S0165-1765(01)00394-9
6. Kurzban R, Houser D. Individual differences in cooperation in a circular public goods game. Eur J Pers. 2001; 15: S37–S52. https://doi.org/10.1002/per.420
7. Sutter M, Untertrifaller A. Children's heterogeneity in cooperation and parental background: An experimental study. Journal of Economic Behavior & Organization. 2020; 171: 286–296. https://doi.org/10.1016/j.jebo.2020.01.010
8. Thöni C, Volk S. Conditional cooperation: Review and refinement. Economics Letters. 2018; 171: 37–40. https://doi.org/10.1016/j.econlet.2018.06.022
9. Cesarini D, Dawes CT, Fowler JH, Johannesson M, Lichtenstein P, Wallace B. Heritability of cooperative behavior in the trust game. PNAS. 2008; 105: 3721–3726. https://doi.org/10.1073/pnas.0710069105 PMID: 18316737
10. Cesarini D, Dawes CT, Johannesson M, Lichtenstein P, Wallace B. Genetic Variation in Preferences for Giving and Risk Taking. Q J Econ. 2009; 124: 809–842. https://doi.org/10.1162/qjec.2009.124.2.809
11. Hiraishi K, Shikishima C, Yamagata S, Ando J. Heritability of decisions and outcomes of public goods games. Front Psychol. 2015; 6. https://doi.org/10.3389/fpsyg.2015.00373 PMID: 25954213
12. Aspé-Sánchez M, Moreno M, Rivera MI, Rossi A, Ewer J. Oxytocin and Vasopressin Receptor Gene Polymorphisms: Role in Social and Psychiatric Traits. Front Neurosci. 2016; 9. https://doi.org/10.3389/fnins.2015.00510 PMID: 26858594
13. Ebstein RP, Israel S, Chew SH, Zhong S, Knafo A. Genetics of Human Social Behavior. Neuron. 2010; 65: 831–844. https://doi.org/10.1016/j.neuron.2010.02.020 PMID: 20346758

14. Benjamin DJ, Cesarini D, Loos MJHM van der, Dawes CT, Koellinger PD, Magnusson PKE, et al. The genetic architecture of economic and political preferences. PNAS. 2012; 109: 8026–8031. https://doi.org/10.1073/pnas.1120666109 PMID: 22566634

15. Chabris CF, Hebert BM, Benjamin DJ, Beauchamp J, Cesarini D, van der Loos M, et al. Most Reported Genetic Associations With General Intelligence Are Probably False Positives. Psychol Sci. 2012; 23: 1314–1323. https://doi.org/10.1177/0956797611435528 PMID: 23012269

16. Duncan LE, Keller MC. A critical review of the first 10 years of candidate gene-by-environment interaction research in psychiatry. Am J Psychiatry. 2011; 168: 1041–1049. https://doi.org/10.1176/appi.ajp.2011.11020191 PMID: 21890791

17. Hewitt JK. Editorial policy on candidate gene association and candidate gene-by-environment interaction studies of complex traits. Behav Genet. 2012; 42: 1–2. https://doi.org/10.1007/s10519-011-9504-z PMID: 21928046

18. Chabris CF, Lee JJ, Benjamin DJ, Beauchamp JP, Glaeser EL, Borst G, et al. Why It Is Hard to Find Genes Associated With Social Science Traits: Theoretical and Empirical Considerations. Am J Public Health. 2013; 103: S152–S166. https://doi.org/10.2105/AJPH.2013.301327 PMID: 23927501

19. Chabris CF, Lee JJ, Cesarini D, Benjamin DJ, Laibson DI. The Fourth Law of Behavior Genetics. Curr Dir Psychol Sci. 2015; 24: 304–312. https://doi.org/10.1177/0963721415580430 PMID: 26556960

20. Visscher PM, Wray NR, Zhang Q, Sklar P, McCarthy MI, Brown MA, et al. 10 Years of GWAS Discovery: Biology, Function, and Translation. The American Journal of Human Genetics. 2017; 101: 5–22. https://doi.org/10.1016/j.ajhg.2017.06.005 PMID: 28686856

21. Andreozzi L, Ploner M, Saral AS. The stability of conditional cooperation: beliefs alone cannot explain the decline of cooperation in social dilemmas. Scientific Reports. 2020; 10: 13610. https://doi.org/10.1038/s41598-020-70681-z PMID: 32788712

22. Gächter S, Thöni C. Social Learning and Voluntary Cooperation among like-Minded People. Journal of the European Economic Association. 2005; 3: 303–314. https://doi.org/10.1162/jeea.2005.3.2–3.303

23. Declerck CH, Boone C. The neuroeconomics of cooperation. Nature Human Behaviour. 2018; 2: 438–440. https://doi.org/10.1038/s41562-018-0387-3 PMID: 31097811

24. Gottesman II, Gould TD. The endophenotype concept in psychiatry: etymology and strategic intentions. Am J Psychiatry. 2003; 160: 636–645. https://doi.org/10.1176/appi.ajp.160.4.636 PMID: 12668349

25. Selten R. Die Strategiemethode zur Erforschung des eingeschrankt rationalen Verhaltens im Rahmen eines Oligopolexperimentes. In: Sauermann H, editor. Beitrage zur experimentellen Wirtschaftsforschung. Tubingen: J.C.B. Mohr (Paul ¨ Siebeck); 1967. pp. 136–168.

26. Baumgartner T, Dahinden FM, Gianotti LRR, Knoch D. Neural traits characterize unconditional cooperators, conditional cooperators, and noncooperators in group-based cooperation. Human Brain Mapping. 2019; 40: 4508–4517. https://doi.org/10.1002/hbm.24717 PMID: 31313437

27. Mertins V, Schote AB, Meyer J. Variants of the Monoamine Oxidase A gene (MAOA) predict free-riding behavior in women in a strategic public goods experiment. Journal of Neuroscience, Psychology, and Economics. 2013; 6: 97–114. https://doi.org/10.1037/a0032877

28. Sabol SZ, Hu S, Hamer D. A functional polymorphism in the monoamine oxidase A gene promoter. Hum Genet. 1998; 103: 273–279. https://doi.org/10.1007/s004390050816 PMID: 9799080

29. Mertins V, Schote AB, Hoffeld W, Griessmair M, Meyer J. Genetic Susceptibility for Individual Cooperation Preferences: The Role of Monoamine Oxidase A Gene (MAOA) in the Voluntary Provision of Public Goods. PLOS ONE. 2011; 6: e20959. https://doi.org/10.1371/journal.pone.0020959 PMID: 21698196

30. Way BM, Lieberman MD. Is there a genetic contribution to cultural differences? Collectivism, individualism and genetic markers of social sensitivity. Soc Cogn Affect Neurosci. 2010; 5: 203–211. https://doi.org/10.1093/scan/nsq059 PMID: 20592043

31. Bachner-Melman R, Ebstein RP. Chapter 4—The role of oxytocin and vasopressin in emotional and social behaviors. In: Fliers E, Korbonits M, Romijn JA, editors. Handbook of Clinical Neurology. Elsevier; 2014. pp. 53–68. https://doi.org/10.1016/B978-0-444-59602-4.00004–6

32. Gong P, Fan H, Liu J, Yang X, Zhang K, Zhou X. Revisiting the impact of OXTR rs53576 on empathy: A population-based study and a meta-analysis. Psychoneuroendocrinology. 2017; 80. https://doi.org/10.1016/j.psyneuen.2017.03.005 PMID: 28343138

33. Tost H, Kolachana B, Hakimi S, Lemaitre H, Verchinski BA, Mattay VS, et al. A common allele in the oxytocin receptor gene (OXTR) impacts prosocial temperament and human hypothalamic-limbic structure and function. PNAS. 2010; 107: 13936–13941. https://doi.org/10.1073/pnas.1003296107 PMID: 20647384

34. Li J, Zhao Y, Li R, Broster LS, Zhou C, Yang S. Association of Oxytocin Receptor Gene (OXTR) rs53576 Polymorphism with Sociality: A Meta-Analysis. PLOS ONE. 2015; 10: e0131820. https://doi.org/10.1371/journal.pone.0131820 PMID: 26121678

35. Nishina K, Takagishi H, Inoue-Murayama M, Takahashi H, Yamagishi T. Polymorphism of the Oxytocin Receptor Gene Modulates Behavioral and Attitudinal Trust among Men but Not Women. PLOS ONE. 2015; 10: e0137089. https://doi.org/10.1371/journal.pone.0137089 PMID: 26444016

36. Feng C, Lori A, Waldman ID, Binder EB, Haroon E, Rilling JK. A common oxytocin receptor gene (OXTR) polymorphism modulates intranasal oxytocin effects on the neural response to social cooperation in humans. Genes, Brain and Behavior. 2015; 14: 516–525. https://doi.org/10.1111/gbb.12234 PMID: 26178189

37. Knafo A, Israel S, Darvasi A, Bachner-Melman R, Uzefovsky F, Cohen L, et al. Individual differences in allocation of funds in the dictator game associated with length of the arginine vasopressin 1a receptor RS3 promoter region and correlation between RS3 length and hippocampal mRNA. Genes, Brain and Behavior. 2008; 7: 266–275. https://doi.org/10.1111/j.1601-183X.2007.00341.x PMID: 17696996

38. Wang J, Qin W, Liu F, Liu B, Zhou Y, Jiang T, et al. Sex-specific mediation effect of the right fusiform face area volume on the association between variants in repeat length of AVPR1ARS3 and altruistic behavior in healthy adults. Hum Brain Mapp. 2016; 37: 2700–2709. https://doi.org/10.1002/hbm.23203 PMID: 27027249

39. Nishina K, Takagishi H, Takahashi H, Sakagami M, Inoue-Murayama M. Association of Polymorphism of Arginine-Vasopressin Receptor 1A (AVPR1a) Gene With Trust and Reciprocity. Front Hum Neurosci. 2019; 13. https://doi.org/10.3389/fnhum.2019.00230 PMID: 31354450

40. Fischbacher U. z-Tree: Zurich toolbox for ready-made economic experiments. Exp Econ. 2007; 10: 171–178. https://doi.org/10.1007/s10683-006-9159-4

41. Tsuchimine S, Yasui-Furukori N, Kaneda A, Saito M, Nakagami T, Sato K, et al. Association between monoamine oxidase A (MAOA) and personality traits in Japanese individuals. Progress in Neuro-Psychopharmacology and Biological Psychiatry. 2008; 32: 1932–1935. https://doi.org/10.1016/j.pnpbp.2008.09.012 PMID: 18845200

42. Wu N, Li Z, Su Y. The association between oxytocin receptor gene polymorphism (OXTR) and trait empathy. Journal of Affective Disorders. 2012; 138: 468–472. https://doi.org/10.1016/j.jad.2012.01.009 PMID: 22357335

43. Avinun R, Israel S, Shalev I, Gritsenko I, Bornstein G, Ebstein RP, et al. AVPR1A Variant Associated with Preschoolers' Lower Altruistic Behavior. PLOS ONE. 2011; 6: e25274. https://doi.org/10.1371/journal.pone.0025274 PMID: 21980412

44. Das M, Bhowmik AD, Sinha S, Chattopadhyay A, Chaudhuri K, Singh M, et al. MAOA promoter polymorphism and attention deficit hyperactivity disorder (ADHD) in indian children. American Journal of Medical Genetics Part B: Neuropsychiatric Genetics. 2006; 141B: 637–642. https://doi.org/10.1002/ajmg.b.30385 PMID: 16856146

45. Lyon MF. X-chromosome inactivation. Current Biology. 1999; 9: R235–R237. https://doi.org/10.1016/s0960-9822(99)80151-1 PMID: 10209128

46. Okbay A, Rietveld CA. On improving the credibility of candidate gene studies: A review of candidate gene studies published in Emotion. Emotion. 2015; 15: 531–537. https://doi.org/10.1037/emo0000076 PMID: 26214572

47. Gächter S, Kölle F, Quercia S. Reciprocity and the tragedies of maintaining and providing the commons. Nature Human Behaviour. 2017; 1: 650–656. https://doi.org/10.1038/s41562-017-0191-5 PMID: 28944297

48. Elfenbein HA, Foo MD, White J, Tan HH, Aik VC. Reading your counterpart: The benefit of emotion recognition accuracy for effectiveness in negotiation. Journal of Nonverbal Behavior. 2007; 31: 205–223. https://doi.org/10.1007/s10919-007-0033-7

49. Krumhuber E, Manstead A, Cosker D, Marshall D, Rosin P, Kappas A. Facial dynamics as indicators of trustworthiness and cooperative behavior. Emotion. 2007; 7: 730–735. https://doi.org/10.1037/1528-3542.7.4.730 PMID: 18039040

50. Sally D, Hill E. The development of interpersonal strategy: Autism, theory-of-mind, cooperation and fairness. Journal of Economic Psychology. 2006; 27: 73–97. https://doi.org/10.1016/j.joep.2005.06.015

51. Miller JH, Butts CT, Rode D. Communication and cooperation. Journal of Economic Behavior & Organization. 2002; 47: 179–195. https://doi.org/10.1016/S0167-2681(01)00159-7

52. Haas BW, Anderson IW, Smith JM. Navigating the complex path between the oxytocin receptor gene (OXTR) and cooperation: an endophenotype approach. Front Hum Neurosci. 2013; 7. https://doi.org/10.3389/fnhum.2013.00801 PMID: 24348360

53. Luo S, Li B, Ma Y, Zhang W, Rao Y, Han S. Oxytocin receptor gene and racial ingroup bias in empathy-related brain activity. NeuroImage. 2015; 110: 22–31. https://doi.org/10.1016/j.neuroimage.2015.01.042 PMID: 25637390

54. Baumgartner T, Heinrichs M, Vonlanthen A, Fischbacher U, Fehr E. Oxytocin Shapes the Neural Circuitry of Trust and Trust Adaptation in Humans. Neuron. 2008; 58: 639–650. https://doi.org/10.1016/j.neuron.2008.04.009 PMID: 18498743

55. Christ CC, Carlo G, Stoltenberg SF. Oxytocin Receptor (OXTR) Single Nucleotide Polymorphisms Indirectly Predict Prosocial Behavior Through Perspective Taking and Empathic Concern. Journal of Personality. 2016; 84: 204–213. https://doi.org/10.1111/jopy.12152 PMID: 25403479

56. Plomin R, DeFries JC, McClearn GE. Behavioral Genetics. Macmillan; 2008.

57. Henrich J. Culture and social behavior. Current Opinion in Behavioral Sciences. 2015; 3: 84–89. https://doi.org/10.1016/j.cobeha.2015.02.001

58. Ioannidis JPA, Patsopoulos NA, Evangelou E. Heterogeneity in Meta-Analyses of Genome-Wide Association Investigations. PLOS ONE. 2007; 2: e841. https://doi.org/10.1371/journal.pone.0000841 PMID: 17786212

59. McCullough ME, Churchland PS, Mendez AJ. Problems with measuring peripheral oxytocin: Can the data on oxytocin and human behavior be trusted? Neuroscience & Biobehavioral Reviews. 2013; 37: 1485–1492. https://doi.org/10.1016/j.neubiorev.2013.04.018 PMID: 23665533

60. Nave G, Camerer C, McCullough M. Does Oxytocin Increase Trust in Humans? A Critical Review of Research. Perspect Psychol Sci. 2015; 10: 772–789. https://doi.org/10.1177/1745691615600138 PMID: 26581735

61. Leng G, Ludwig M. Intranasal Oxytocin: Myths and Delusions. Biological Psychiatry. 2016; 79: 243–250. https://doi.org/10.1016/j.biopsych.2015.05.003 PMID: 26049207

62. Walum H, Waldman ID, Young LJ. Statistical and Methodological Considerations for the Interpretation of Intranasal Oxytocin Studies. Biological Psychiatry. 2016; 79: 251–257. https://doi.org/10.1016/j.biopsych.2015.06.016 PMID: 26210057

63. Kosfeld M, Heinrichs M, Zak PJ, Fischbacher U, Fehr E. Oxytocin increases trust in humans. Nature. 2005; 435: 673–676. https://doi.org/10.1038/nature03701 PMID: 15931222

64. Zak PJ, Kurzban R, Matzner WT. Oxytocin is associated with human trustworthiness. Hormones and Behavior. 2005; 48: 522–527. https://doi.org/10.1016/j.yhbeh.2005.07.009 PMID: 16109416

65. Mierop A, Mikolajczak M, Stahl C, Béna J, Luminet O, Lane A, et al. How Can Intranasal Oxytocin Research Be Trusted? A Systematic Review of the Interactive Effects of Intranasal Oxytocin on Psychosocial Outcomes. Perspect Psychol Sci. 2020; 15: 1228–1242. https://doi.org/10.1177/1745691620921525 PMID: 32633663

66. Krueger F, Parasuraman R, Iyengar V, Thornburg M, Weel J, Lin M, et al. Oxytocin Receptor Genetic Variation Promotes Human Trust Behavior. Front Hum Neurosci. 2012; 6. https://doi.org/10.3389/fnhum.2012.00004 PMID: 22347177

67. Apicella CL, Cesarini D, Johannesson M, Dawes CT, Lichtenstein P, Wallace B, et al. No Association between Oxytocin Receptor (OXTR) Gene Polymorphisms and Experimentally Elicited Social Preferences. Lalueza-Fox C, editor. PLoS ONE. 2010; 5: e11153. https://doi.org/10.1371/journal.pone.0011153 PMID: 20585395

68. Duncan LE, Ostacher M, Ballon J. How genome-wide association studies (GWAS) made traditional candidate gene studies obsolete. Neuropsychopharmacology. 2019; 44: 1518–1523. https://doi.org/10.1038/s41386-019-0389-5 PMID: 30982060

69. Linnér RK, Biroli P, Kong E, Meddens SFW, Wedow R, Fontana MA, et al. Genome-wide association analyses of risk tolerance and risky behaviors in over 1 million individuals identify hundreds of loci and shared genetic influences. Nature Genetics. 2019; 51: 245–257. https://doi.org/10.1038/s41588-018-0309-3 PMID: 30643258

70. Okbay A, Baselmans BML, De Neve J-E, Turley P, Nivard MG, Fontana MA, et al. Genetic variants associated with subjective well-being, depressive symptoms, and neuroticism identified through genome-wide analyses. Nature Genetics. 2016; 48: 624–633. https://doi.org/10.1038/ng.3552 PMID: 27089181

71. Rietveld CA, Medland SE, Derringer J, Yang J, Esko T, Martin NW, et al. GWAS of 126,559 Individuals Identifies Genetic Variants Associated with Educational Attainment. Science. 2013; 340: 1467–1471. https://doi.org/10.1126/science.1235488 PMID: 23722424

72. Sniekers S, Stringer S, Watanabe K, Jansen PR, Coleman JRI, Krapohl E, et al. Genome-wide association meta-analysis of 78,308 individuals identifies new loci and genes influencing human intelligence. Nature Genetics. 2017; 49: 1107–1112. https://doi.org/10.1038/ng.3869 PMID: 28530673

73. de Moor MHM, Costa PT, Terracciano A, Krueger RF, de Geus EJC, Toshiko T, et al. Meta-analysis of genome-wide association studies for personality. Molecular Psychiatry. 2012; 17: 337–349. https://doi.org/10.1038/mp.2010.128 PMID: 21173776

74. Brunnlieb C, Nave G, Camerer CF, Schosser S, Vogt B, Münte TF, et al. Vasopressin increases human risky cooperative behavior. PNAS. 2016; 113: 2051–2056. https://doi.org/10.1073/pnas.1518825113 PMID: 26858433

75. Israel S, Lerer E, Shalev I, Uzefovsky F, Riebold M, Laiba E, et al. The Oxytocin Receptor (OXTR) Contributes to Prosocial Fund Allocations in the Dictator Game and the Social Value Orientations Task. PLOS ONE. 2009; 4: e5535. https://doi.org/10.1371/journal.pone.0005535 PMID: 19461999

76. Zhong S, Israel S, Shalev I, Xue H, Ebstein RP, Chew SH. Dopamine D4 Receptor Gene Associated with Fairness Preference in Ultimatum Game. PLOS ONE. 2010; 5: e13765. https://doi.org/10.1371/journal.pone.0013765 PMID: 21072167

77. Chew SH, Ebstein RP, Zhong S. Sex-hormone genes and gender difference in ultimatum game: Experimental evidence from China and Israel. Journal of Economic Behavior & Organization. 2013; 90: 28–42. https://doi.org/10.1016/j.jebo.2013.03.008

78. Reuter M, Felten A, Penz S, Mainzer A, Markett S, Montag C. The influence of dopaminergic gene variants on decision making in the ultimatum game. Front Hum Neurosci. 2013; 7. https://doi.org/10.3389/fnhum.2013.00242 PMID: 23759976

79. Schroeder KB, McElreath R, Nettle D. Variants at serotonin transporter and 2A receptor genes predict cooperative behavior differentially according to presence of punishment. PNAS. 2013; 110: 3955–3960. https://doi.org/10.1073/pnas.1216841110 PMID: 23431136

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CONTRIBUTED PAPER

Effects of experience with access regimes on stewardship behaviors of small-scale fishers

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Abstract

Governance regimes that assign exclusive access to support collective action are increasingly promoted to manage common-pool resources under the premise that they foster environmental stewardship. However, experimental evidence linked to existing policies that support this premise is lacking. Overlapping access policies in small-scale fisheries provide a unique opportunity to test the effects of access regimes on users' stewardship behaviors. We performed a lab-in-the-field experiment to assess how fishers' previous experience with access regimes relates to compliance and peer enforcement ($n = 120$). Fishers' compliance and peer-enforcement decisions were compared in a common-pool-resource game. Treatments differed in framing to represent exclusive access and pseudo-open access regimes, both of which fishers face in real life. To contrast behavior in the game with real-life observations, we compared fishers' associations that have shown relatively high and low management performance under exclusive access policies. Compliance and peer enforcement were higher under the exclusive access treatment than under the pseudo-open access treatment only for fishers' associations with high management performance in real life. Behaviors in the game reflected differences between associations in real life. Our results support previous research on ocean governance by experimentally assessing the role of access regimes in determining users' stewardship and suggest potential mechanisms for stewardship internalization.

KEYWORDS
collective action, environmental stewardship, external validity, lab-in-the-field experiment, small-scale fisheries, territorial user rights for fisheries

Efectos de la experiencia con regímenes de acceso sobre comportamientos de gestión responsable de pescadores a pequeña escala

Resumen: Las políticas que asignan acceso exclusivo a grupos de usuarios para apoyar la acción colectiva son cada vez más promovidas para el manejo de recursos de uso comunitario bajo la premisa de que fomentan la gestión ambiental responsable. Sin embargo, la evidencia experimental vinculada a políticas existentes que respalde esta premisa es insuficiente. La superposición de diversas políticas de acceso en las pesquerías a pequeña escala proporciona una oportunidad única para analizar los efectos de los regímenes de acceso sobre el comportamiento de gestión de los usuarios. Realizamos un experimento, llevando el laboratorio al campo, para evaluar cómo la experiencia previa de los pescadores con regímenes de acceso se relaciona con sus comporatamientos de cumplimiento y de sanción de pares ($n = 120$). Comparamos el cumplimiento con cutoas de extracción de los pescadores y sus decisiones de sancionar a pares que incumplian las cuotas en un juego de recursos de uso comunitario entre dos tratamientos. Los tratamientos variaban en la contextualización del juego para representar una pesquería de acceso exclusivo y una de pseudo libre acceso, a las que se enfrentan los pescadores en la vida real. Para contrastar el comportamiento en el juego con las observaciones de la vida real, comparamos los resultados de asociaciones de pescadores que han mostrado un desempeño de manejo relativamente alto y bajo con las políticas de acceso exclusivo. El cumplimiento y la sanción de pares fueron mayores bajo el tratamiento de acceso exclusivo que bajo el de pseudo libre acceso sólo para aquellas asociaciones de pescadores con un alto desempeño de manejo en la vida real. Los comportamientos en el juego reflejaron las diferencias entre las asociaciones en la vida real. Nuestros resultados respaldan investigaciones previas sobre la governanza de recursos marinos mediante la evaluación experimental del papel que tienen las políticas de acceso en la determinación de la gestión del usuario y sugieren mecanismos potenciales para la internalización de dicha gestión.

PALABRAS CLAVE
acción colectiva, derechos de uso territorial para las pesquerías, experimento de campo, gestión ambiental, pesquería a pequeña escala, validez externa

INTRODUCTION

Environmental stewardship is a promising pathway toward the sustainable use and conservation of natural common-pool resources (CPRs) (Bennett et al., 2018). Local environmental stewardship can trigger the protection and responsible harvest of CPRs and avert “the tragedy of the commons” (Bennett et al., 2018; Ostrom, 1990). Compliance with appropriation rules and peer enforcement are stewardship behaviors linked to successful conservation and management outcomes across ecosystems (Bergseth et al., 2015; Ostrom, 1990; Rustagi et al., 2010; Wright et al., 2016). Therefore, identifying policies that enhance user compliance and peer enforcement is an important step to advance the conservation of CPRs. An approach increasingly applied to foster these behaviors among CPRs users is the establishment of formal, collective, and exclusive access regimes (CEARs) (Nguyen Thi Quynh et al., 2017). These regimes grant legal rights to a group of users to exclusively access, use, and manage resource stocks (Schlager & Ostrom, 1992). In theory, CEARs incentivize environmental stewardship relative to open access (OA) resource use by securing future benefits to those investing in a stock’s sustainability and involving users in decision-making (Jentoft et al., 1998; Wilen et al., 2012).

Achieving sustainability by implementing CEARs rests, in part, on the assumption that formal access rights promote user compliance and peer enforcement. However, research shows mixed results regarding the relationship between access policies and local environmental stewardship (e.g., Gelcich et al., 2006; Gilmour et al., 2012; McDonald et al., 2020). This mixed performance is likely the consequence of the lack of counterfactuals (van Putten et al., 2014), reliance on self-reported behaviors prone to biases, especially when involving sensitive behaviors such as compliance (Gavin et al., 2010), and case studies encompassing a range of resource systems operating under different institutional and legal settings (van Putten et al., 2014; Gelcich et al., 2019). Experimental economics provides a complementary approach to assess the determinants of human behaviors by controlling for confounding variables (Smith, 1982; Ostrom, 2006). Moreover, by attaching financial consequences to decisions, economic experiments reduce the biases inherent to self-reporting (Smith, 1982). To recreate the collective-action problem faced by CPR users, researchers use CPR games. Insights from lab-in-the-field experiments based on CPR games have increased the robustness of findings from case studies and helped uncover the role of institutional arrangements in CPR use (Ostrom, 2006; Cardenas, 2011). Behaviors displayed by users in these experiments have been proven to relate to real-life observations supporting the external validity of this approach (Rustagi et al., 2010; Carpenter & Seki, 2011; Gelcich et al., 2013; Basurto et al., 2016). Accordingly, lab-in-the-field experiments constitute an appealing way to unpack the relationship between access regimes and local environmental stewardship.

Small-scale fisheries are CPRs for which compliance and peer enforcement are particularly important given the difficulty of establishing effective centralized management and enforcement (Costello et al., 2012; Donlan et al., 2020). Small-scale fisheries can be managed through different and overlapping access regimes, depending on the different target species, and therefore provide a unique opportunity to test the role of access policies in determining local stewardship. In central Chile, fishers operate in at least two distinct fishery-management access regimes: a CEAR that takes the form of territorial user rights for fisheries (TURFs) granted to fishers’ associations to harvest benthic resources and a pseudo-OA regime for demersal fish species. We empirically assessed how Chilean fishers’ experience with formal CEARs relates to compliance and peer enforcement with a between-subjects lab-in-the-field experiment.

We compared behaviors of fishers in CPR games conducted under two treatments that involved the same monetary incentives but differed in framing to represent a fishery that is managed under CEAR and another that operates as pseudo-OA. To assess the external validity of our experiment, we considered two types of fishers’ associations depending on their real-life performance (high or low) with CEAR.

Assuming standard rationality, the predicted outcomes for the game were no compliance and no peer enforcement. However, deviations from rationality are common in social dilemmas such as CPRs due to subjects’ internalized expectations and norms (e.g., Cárdenas & Ostrom, 2004; Rustagi et al.,

TABLE 1 Between-subjects design of an experiment that compares behaviors of fishers in a common-pool-resource game under two treatments that differ in framing to represent the loco fishery, which is managed under collective and exclusive access, and the hake fishery, which operates under pseudo-open access. Fishers were recruited from associations that have shown signs of relatively high and low performance under collective and exclusive access

	Collective and exclusive access regime (Loco frame)		Pseudo-open access (Hake frame)	
Treatment **Association type**	**Unenforced stage (first 10 rounds)**	**Peer-enforced stage (last 10 rounds)**	**Unenforced stage (first 10 rounds)**	**Peer-enforced stage (last 10 rounds)**
High performance	30 (six groups of five players)		30 (six groups of five players)	
Low performance	30 (six groups of five players)[a]		30 (six groups of five players)[a]	

[a] In two of the 12 game sessions, groups were randomly reallocated in each round (Appendix S5). Because subjects were unaware of the reallocation, behaviors should not differ from those expected in fixed groups. Subjects in these sessions potentially interacted with all the other nine subjects in the session. Therefore, to obtain independent observations, we computed the group mean compliance and probability of reporting across all 10 subjects in each of these two sessions.

2010; Fehr & Schurtenberger, 2018). Based on the premise that exclusive access favors the internalization of stewardship, we expected compliance and peer enforcement to be higher under the CEAR treatment than under the pseudo-OA treatment for high-performance associations. If our experiments were externally valid, high-performance associations would exhibit more compliance and peer enforcement than low-performance associations under the CEAR treatment but not necessarily under pseudo-OA. We additionally evaluated how peer enforcement affects compliance and explored the role of expectations and norms in the different settings.

METHODS

Implementation

In the CEAR treatment, the game was framed as the harvest of loco (*Concholepas concholepas*), which is harvested within TURFs (Gelcich et al., 2010). In the pseudo-OA treatment, the game was framed as the fishing of hake (*Merluccius gayi*), which is fished in a quota scheme that operates as pseudo-OA due to poor enforcement and unclear stock boundaries (Plotnek et al., 2016; Oyanedel et al., 2020). Fishers were recruited from fishers' associations that targeted loco and hake, were located <200 km apart to minimize geographical differences (Appendix S1), and could be categorized ex ante into high-performance and low-performance depending on their real-life performance with CEAR. We recruited a total of 120 fishers from two high-performance and three low-performance associations. Associations were categorized as having high or low performance with CEARs according to a TURF-performance index developed by Marín et al. (2012). The index includes indicators of fishers' pride in their TURF, compliance with TURF rules, trends of annual TURF quotas, and third-party assessments of TURF management (Appendix S2). All these variables are related to collective action in TURF management. We conducted 12 sessions, two in each association (one with each frame), except for one high-performance association in which we conducted four sessions (two with each frame). Half the fishers in each association were randomly assigned to the CEAR treatment and half were to the pseudo-OA treatment. The experimental design is summarized in Table 1.

In each session, 10 fishers from the same association entered the room and seated themselves in front of an individual laptop. A facilitator informed the subjects that they would play 20 rounds of a CPR game in fixed groups of five, randomly and anonymously assembled by the software. Subjects were also informed that decisions would be recorded anonymously and that they could leave the experiment at any time. After the instructions were read, subjects played three trial rounds. Game instructions were identical for both treatments except for the words used to describe the resource units (i.e., *number of locos* or *kilos of hake*), the action (i.e., *harvesting* or *fishing*), and the enforcement authority (i.e., *association's board* or *National Service of Fisheries*) (Appendix S3). The game was programmed in z-Tree (Fischbacher, 2007), and no communication was allowed. Once a session was completed, fishers left the room to receive their payments in private and the next group entered the room, thus avoiding communication. We obtained informed consent from all participants. Our protocol was approved by the ethics committee of Pontificia Universidad Católica de Chile.

The CPR game

At the beginning of each round $t \in \{0, \dots, 9\}$, each fisher was given 100 units of the resource representing their individual quota, which was assumed to be harvested completely. Then, simultaneously, each fisher $i \in \{1, \dots, 5\}$ had to privately decide the $x \in \{0, \dots 50\}$ number of units to harvest above their quota (i.e., overharvest). There was a negative externality to mimic the cost that overharvest imposes on other users in real life. For each unit that a fisher decided to overharvest, all other members of their group $(j \in \{1, \dots, 5\} \neq i)$ lost half a unit. The unitary price of a unit was \$10 CLP (US\$ ~0.014). The individual payment per round was given by

$$\pi_{i,t} = \left(100 + x_{i,t} - \frac{1}{2}\sum_{j \in S_{-i}} x_{j,t}\right) \times \$10. \tag{1}$$

The first 10 rounds of the game constituted the unenforced stage. At the beginning of the 11th round, the peer-enforced stage started, and a peer-enforcement mechanism was introduced unexpectedly and permanently. In the remaining rounds, once all fishers had entered their overharvest, two fishers were randomly assigned as inspectors and randomly and anonymously assigned to inspect another group member. The harvest of the inspected fisher was revealed to their inspector, and if overharvest was >0, the inspector had the opportunity to report the offender. Inspectors were never assigned to inspect themselves and subjects were aware of this. Once an offender was reported, their harvest for the round was seized. This mechanism recreates fishers' real-life decisions on whether to report noncompliance to authorities. Once inspectors entered their decisions, a summary screen revealed to each fisher their harvest, others' mean harvest, the number of units lost due to others' overharvest, their earnings, and whether their harvest was seized due to a peer's report. To recreate the payment a fisher would earn for patrolling, we added $250 CLP to a fisher's account each time they were appointed as an inspector. Because reporting a peer is costly in real life, inspectors had to pay $250 CLP to report.

The expected outcomes for the game differed under different models of behavior. Assuming standard rationality, the game equilibrium in the unenforced stage is a tragedy of the commons in which each subject overharvests the maximum and earns the minimum (Gelcich et al., 2013). Complying and reporting are rational decisions in the peer-enforced stage only if subjects expect high levels of others' compliance (above 80%) and a high probability of being reported (above 0.83) (Appendix S4). Models of other-regarding preferences can account for compliance and engagement in peer enforcement. For example, under models of negative reciprocity subjects are willing to pay for leveling of payments (Rabin, 1993; Fehr & Gächter, 2000). Similarly, subjects are willing to pay to sanction prejudicial behavior under inequity aversion (Fehr & Schmidt, 1999; Bolton & Ockenfels, 2000). Alternatively, models of altruism predict compliance and a lack of reports because altruistic subjects will refrain from reducing their peers' payments (Andreoni, 1990). More important for our study, however, is that most models predict no differences between settings with the same monetary payments, such as our treatments, unless they consider context-specific parameters, expectations, or norms (Dufwenberg et al., 2011; Ellingsen et al., 2012).

Statistical analyses

We operationalized compliance as the percentage of resource units that were not overharvested (i.e., an overharvest of 50 units corresponded to 0% compliance and an overharvest of 0 units to 100% compliance). Peer enforcement was assessed as the probability of reporting (i.e., the number of reports divided by the number of opportunities to report). We aggregated individual behavior over the rounds and used nonparametric analyses to test the differences. We ran pairwise comparisons of the individual mean percent compliance and the individual probability of reporting between treatments for each association type and between association types under each treatment. We also compared the individual mean percent compliance between the unenforced and peer-enforced stages and between the first and last round in each treatment–stage–association type combination. We used the Wilcoxon test with two-sided hypotheses testing for each comparison. We adjusted *p*-values for multiple hypotheses testing within each set of comparisons with the Bonferroni correction at a 5% significance level.

We additionally applied a parametric approach, which provides greater power to test whether our results held when observations were aggregated at the group level in every round. We ran different specifications of ordinary least squared regressions (OLS) with robust standard errors to test the effects of experimental variables on compliance and peer enforcement. The independent variable for compliance was the group percent compliance in each round and for peer enforcement was the group probability of reporting in each round. The different OLS specifications sequentially included blocks of explanatory variables to check for the stability of coefficients across specifications and to disaggregate the effects of interacting variables. Explanatory variables used in the OLSs for compliance included dummies for the CEAR treatment, high-performance associations, and the peer-enforced stage; continuous variables to enumerate the rounds in the unenforced and peer-enforced stages (from 0 to 9); and interactions of these variables. In OLSs for peer enforcement, explanatory variables included dummies for the CEAR treatment, low-performance associations, and high-performance associations. We also included two control variables—a variable enumerating the round of the peer-enforced stage (from 0 to 9) and the mean overharvest of the inspected fisher in each group and round.

In the main text, we discuss only effects that were consistent across model specifications and report the results of the most parsimonious OLS for compliance and peer enforcement, which were selected based on Akaike's information criterion. In two of the 12 sessions, groups were randomly reallocated in each round (Appendix S5). Because subjects were unaware of the reallocation, behaviors should not differ from those expected in fixed groups. Subjects in these sessions potentially interacted with all the other nine subjects in the session. Therefore, to obtain independent observations, we computed the group mean compliance and probability of reporting across all 10 subjects in each of these two sessions. We added weights to the OLS based on the number of players aggregated in each observation. To assess how others' decisions affected individual compliance and peer enforcement, we ran a linear mixed model and a Probit model, respectively, for each treatment–association type combination (Appendix S6).

RESULTS

Differences in compliance

Compliance was higher under the CEAR treatment than under the pseudo-OA treatment for high-performance associations, which presented a mean individual percent compliance of 72% under the CEAR treatment and 44% under the pseudo-OA treatment (Wilcoxon test, $W = 965$, adjusted $p < 0.01$,

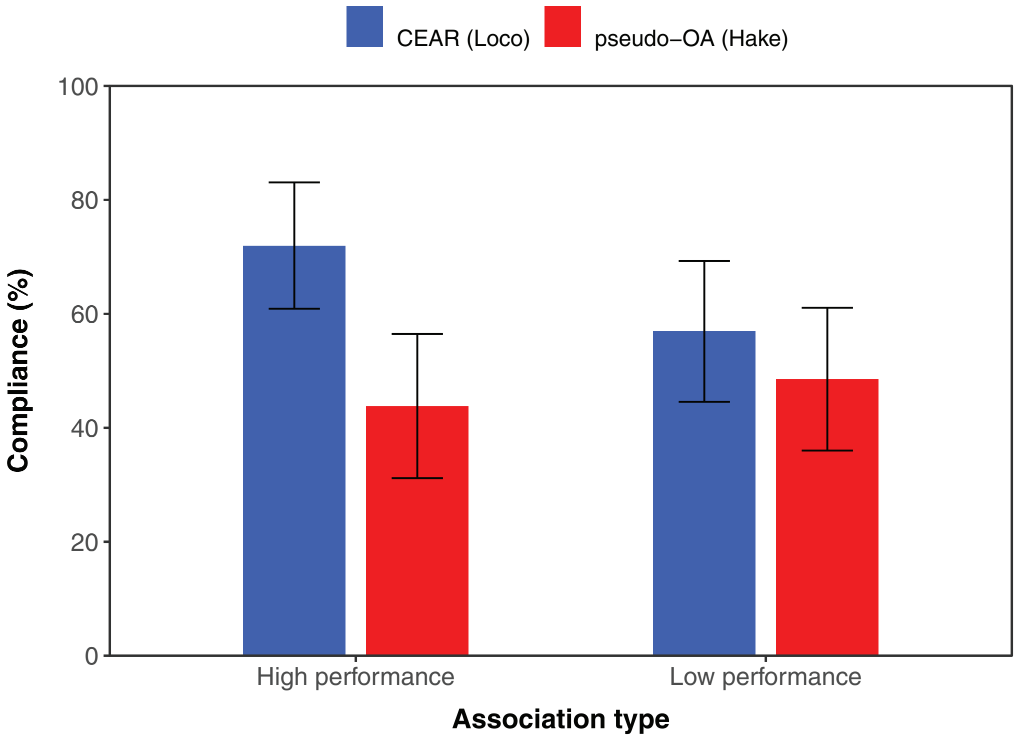

FIGURE 1 Mean percent compliance in the common-pool-resource game with the individual quota of loco, which is fished under collective, exclusive access (CEAR) in real life and with the individual quota of hake, which is fished under pseudo-open access (OA) in real life for high-performance associations and low-performance associations (error bars, 95% CIs computed at the individual level; $n = 30$).

$n = 60$) (Figure 1). In the case of low-performance associations, the mean individual percent compliance was 57% and 49% under the CEAR and pseudo-OA treatments, respectively, and there were no statistically significant differences (Appendix S7).

Strategies of players that chose to comply in every round (i.e., overharvest zero in every round) were revealing regarding motivations toward compliance. We found that in high-performance associations, 10 subjects chose to comply in every round under the CEAR treatment and only two applied this strategy under the pseudo-OA treatment (Fisher exact test, adjusted $p = 0.042$, $n = 60$). This difference was not significant in low-performance associations.

Differences in compliance between high- and low-performance associations under the CEAR treatment reflected real-life differences regarding success with CEAR. The mean individual percent compliance was significantly higher in high-performance associations compared with low-performance associations under the CEAR treatment ($W = 2362.5$, adjusted $p = 0.02$, $n = 60$) (Figure 1) but not under the pseudo-OA regime treatment (Appendix S7).

The most parsimonious OLS showed that the mean group percent compliance was almost 20% higher in high-performance associations under the CEAR treatment relative to the other treatment–association type combinations (CEAR × high-performance association = 19.81, $p < 0.001$, 95% confidence interval [CI]: 10.03–29.59 in model 5) (Appendix S8).

Differences in peer enforcement

Peer enforcement was higher under the CEAR treatment than under the pseudo-OA treatment (Figure 2). However, statistical differences were weaker than for compliance behavior. For high-performance associations, the mean individual probability of reporting was 0.70 under the CEAR treatment and 0.41 under the pseudo-OA treatment. This difference was significant but did not survive correction for multiple hypotheses testing ($W = 215.5$, $p = 0.03$, adjusted $p = 0.11$). In the case of low-performance associations, the mean individual probability of reporting was 0.31 and 0.19 under the CEAR and the pseudo-OA treatments, respectively, with no significant differences between treatments (Appendix S9).

Differences in peer enforcement between association types reflected real-life differences with CEAR. The mean individual probability of reporting under the CEAR treatment was significantly higher in high-performance associations compared with low-performance associations ($W = 476.0$, adjusted $p = 0.02$) (Figure 2). In the case of the pseudo-OA treatment, differences between association types did not survive correction for multiple hypotheses testing ($W = 560.5$, $p = 0.02$, adjusted $p = 0.06$).

The most parsimonious OLS revealed that the group probability of reporting was significantly higher under the CEAR treatment for high-performance associations compared with the other treatment–association type combinations (CEAR × high-performance association = 0.24, $p < 0.05$, 95%

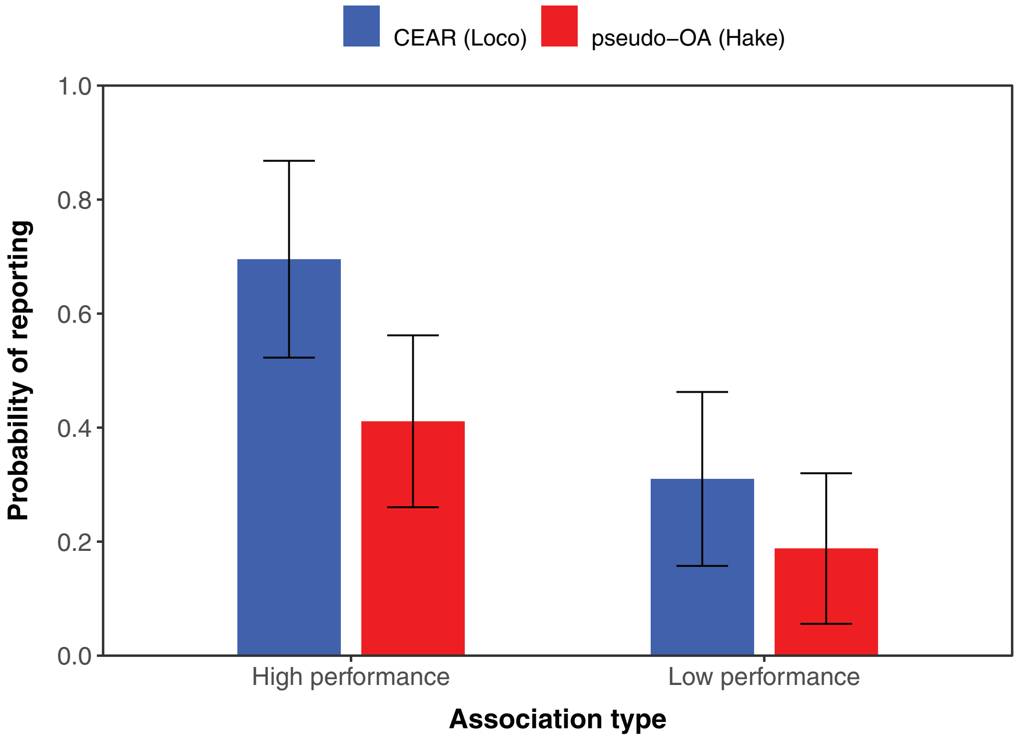

FIGURE 2 Mean probability of reporting a peer to authorities in the common-pool-resource game due to noncompliance with the individual quota of loco, which is fished under collective, exclusive access (CEAR) in real life, and due to noncompliance with the individual quota of hake, which is fished under pseudo-open access (OA) in real life for high-performance associations and low-performance associations (error bars, 95% CIs computed at the individual level). Sample sizes differ because the inspector role was randomly assigned in each round and inspectors could only report if the inspected fisher had overharvested. Therefore, not every fisher had an opportunity to report (for high-performance associations under CEAR treatment, $n = 22$; for high-performance associations pseudo-open access treatment, $n = 30$; for low-performance associations under CEAR treatment, $n = 30$; for low-performance associations under pseudo-open access treatment, $n = 28$)

CI: 0.03–0.46 in model 5; no overlap between the 95% CI of CEAR × high-performance association and other coefficients in model 7) (Appendix S10).

Effect of peer enforcement on compliance

There were no significant differences in the mean individual percent compliance between the unenforced and peer-enforced stages (Appendix S7). Nonetheless, peer enforcement averted the decline of compliance under the CEAR treatment for high-performance associations (Figure 3). In this case, the mean individual percent compliance was 80% in the first round of the unenforced stage and significantly declined to around 60% by the end of the unenforced stage (paired Wilcoxon test comparing the first and last round in the unenforced stage, $W = 147$, adjusted $p < 0.01$, $n = 60$). In the peer-enforced stage, high-performance associations under the CEAR treatment restored high levels of compliance, which remained unchanged until the end of the game (Appendix S11). No significant changes in the mean individual percent compliance occurred within stages for the other treatment–association type combinations (Appendix S11).

A marginally significant decline in compliance during the unenforced stage was confirmed by the most parsimonious OLS with observations aggregated at the group level (unenforced rounds $= -1.10$, $p = 0.06$, 95% CI: -2.36 to 0.16 in model 5) (Appendix S8). Peer enforcement generated a net earnings loss in all the treatment–association type combinations (Appendix S12). The highest aggregated losses occurred in high-performance associations under the CEAR treatment, but losses, in this case, tended to decrease over rounds (Appendix S13).

Discussion

Identifying policy levers to promote environmental stewardship among users is necessary to prevent CPRs degradation in the absence of effective centralized management. We found evidence that access policies governing resource extraction can influence users' compliance and peer enforcement. Our results showed that fishers who experienced effective management under CEAR displayed higher stewardship in a CPR game framed as the harvest of loco, which operates under CEAR in real life, than in the same game framed as the fishing of hake, which operates under pseudo-OA. Although this result supports the role of formal CEARs in promoting users' stewardship behaviors, our results also showed that CEARs alone did not guarantee the internalization of environmental stewardship. This was confirmed by the relatively low stewardship displayed by low-performance associations under the CEAR treatment.

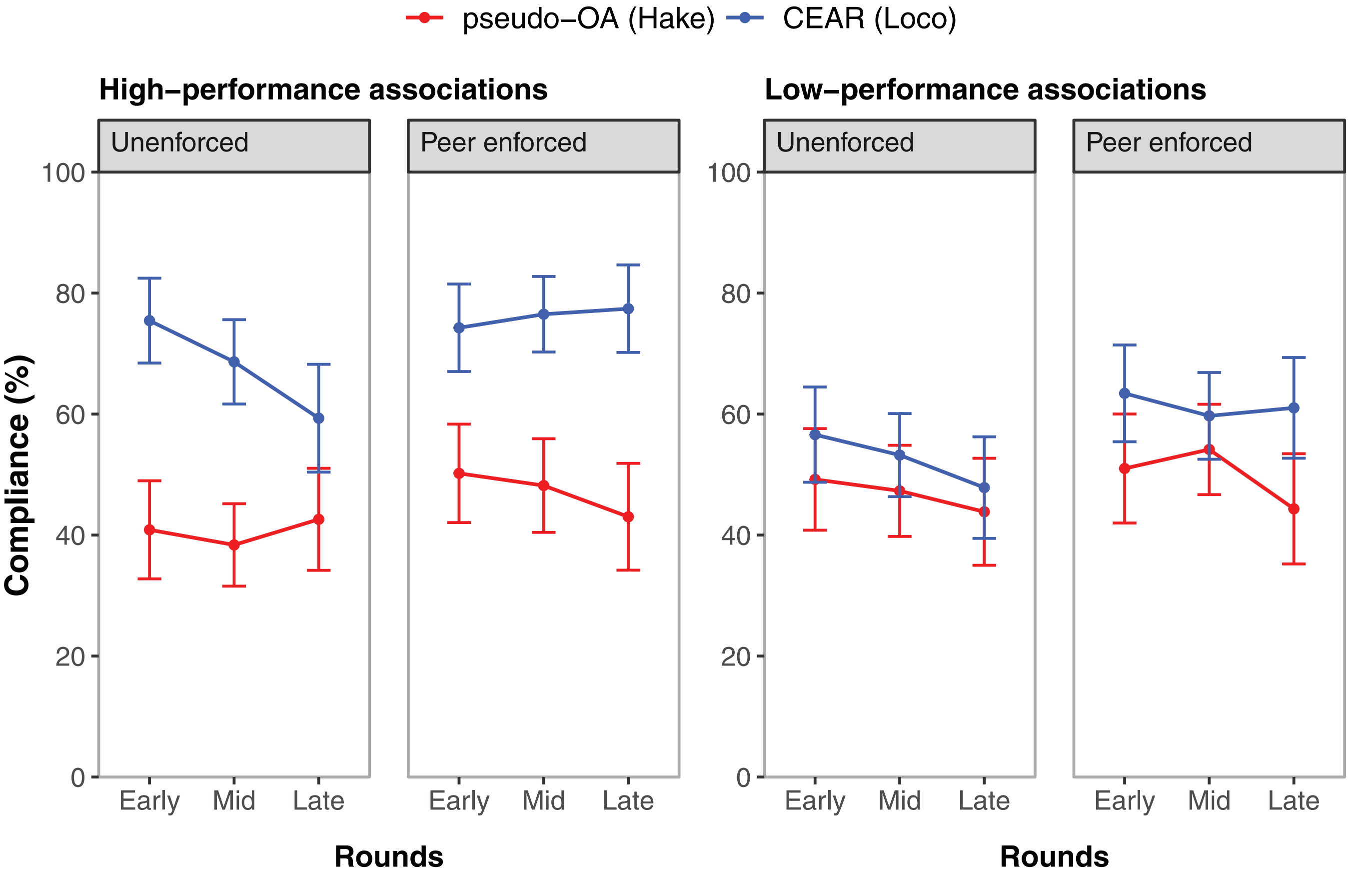

FIGURE 3 Mean percent compliance in the common-pool-resource game with the individual quota of loco, which is fished under collective, exclusive access (CEAR) in real life, and with the individual quota of hake, which is fished under pseudo-open access (OA) in real life for high-performance associations and low-performance associations in early (rounds 1, 2, and 3), middle (rounds 4, 5, 6, and 7), and late (rounds 8, 9, and 10) rounds of the unenforced and peer-enforced stages of the game (error bars, 95% CIs computed at the individual level; $n = 30$)

Our results provide experimental support consistent with observations that suggest that CEAR policies motivate fishers' local stewardship (Gelcich et al., 2010; McDonald et al., 2020). We found that for the same group of users, stewardship increased under the CEAR treatment relative to the pseudo-OA treatment. Our experimental approach accounted for potential selection biases that have raised concerns relative to previous studies in which stewardship behaviors were compared across access regimes with different samples (van Putten et al., 2014). Although we cannot establish a causal link between CEARs and increased local stewardship, our results suggest a role in shaping users' incentives toward stewardship. Similar results support the broader idea that the institutions that people deal with in their daily activities shape their capacity for collective action (Cárdenas & Ostrom, 2004; Leibbrandt et al., 2013; Bouma & Ansink, 2013).

Differences in behaviors observed in our experiment are arguably influenced by the expectations and norms that different fishers hold under each access regime. The levels of compliance observed in the first round suggest that the highest expectations about others' compliance occurred in high-performance associations under a CEAR treatment. On expecting high compliance from other group members, these fishers started with high levels of compliance in accordance with common reciprocation principles (Fehr & Schurtenberger, 2018). These expectations of high compliance are likely shaped by these fishers' real-life experience harvesting loco under effective CEAR (Cárdenas & Ostrom, 2004). Similar framing effects on expectations are reported in the experimental economics literature (Ellingsen et al., 2012).

Several fishers engaged in peer enforcement; it is common in social dilemmas such as CPRs games (Chaudhuri, 2011; Fehr & Schurtenberger, 2018). This cannot be justified by standard rationality in our game. Although reciprocity and inequity aversion could explain reporting decisions, they do not account for the differences between frames. The high levels of peer enforcement observed for high-performance associations under the CEAR treatment could be signaling the presence of social norms for cooperation (Fehr & Schurtenberger, 2018). These norms are theorized to be crucial for effective management under CEAR (Ostrom, 1990, 1998; Jentoft et al., 1998). Treatments did not differ in payments and strategic behavior cannot explain complete restrain from overharvesting. Thus, differences in the number of fishers that complied in every round suggest the presence of internalized norms in these settings. Our results are consistent with evidence from experiments that show norms are sensitive to framing (Krupka & Weber, 2013; Bouma & Ansink, 2013) and evidence from the field that shows that normative motivations relate to compliance of small-scale fishers (Oyanedel et al., 2020).

Peer enforcement did not affect mean levels of compliance as predicted by standard rationality. Nonetheless, in high-performance associations under CEAR, peer enforcement was key to averting the decline of compliance observed in the unenforced stage. This result is consistent with observations from experiments and the field that underscore the role of peer enforcement in sustaining collective action (Ostrom, 1990; Rustagi et al., 2010; Wright et al., 2016). The net earnings loss generated by the peer-enforcement mechanism is common in social dilemmas (Chaudhuri, 2011). Peer enforcement was particularly costly in high-performance associations under the CEAR treatment due to the high frequency and size of the confiscations. Nonetheless, net losses declined over the rounds for this setting, indicating that peer enforcement could become efficient in the long run (Gächter et al., 2008).

Correlates of individual decisions in high-performance associations under the CEAR treatment support the idea that norms and expectations guide stewardship behaviors (Appendix S6). On average, subjects behaved as conditional cooperators, adjusting their compliance to that displayed by others in the previous round. Because the match between one's and others' compliance presented a selfish bias, cooperation declined as subjects updated their expectations (Fehr & Schurtenberger, 2018). In the peer-enforced stage, the average strategy switched from conditional to unconditional compliance, showing that peer enforcement created an effective enforcement alternative that relieved subjects from having to overharvest to retaliate for the low levels of compliance of their peers (Andreoni, 1995). Interestingly, compliance was sustained by the presence of peer enforcement rather than by the actual implementation of reports because subjects did not adjust their compliance after being reported. Subjects either internalized the compliance norm in the presence of peer enforcement or anticipated a high probability of being reported that deterred them from overharvesting. Under the observed probability of reporting, peer enforcement cannot deter a rational subject from overharvesting. Therefore, the most likely explanation is norm internalization. This norm seems to mandate full compliance with the quota because the probability of reporting did not scale with the number of units overharvested.

Our experimental design involved trade-offs between simulating real life and the ability to make unbiased inferences. For example, the use of an alternative design in which the words for the managing authority (i.e., *association's board* or *National Service of Fisheries*) and the species (i.e., *loco* or *hake*) varied separately could have helped isolate the effects of each element in the frame. However, some of the resulting frames would have lacked parallels in real life. Similarly, to recreate the real-life situation of reporting, the peer-enforcement mechanism in our game involved a binary decision that only allowed for the punishment of defectors. Incorporating stock dynamics could have made the game more realistic but would have also made it more difficult to understand, hindering the interpretation of the observed behavior. All these features may affect behavior. Static, repeated dilemmas facilitate cooperation relative to dynamic ones (Vespa, 2020) and allowing for the punishment of cooperators can reduce cooperation (Herrmann et al., 2008). Gradual sanctions may increase cooperation relative to binary systems (Couto et al., 2020). Nonetheless, our focus was not on the levels of cooperation per se, but on the relative differences between frames and samples.

Our results highlight that framing is a crucial feature of lab-in-the-field experiments (Alekseev et al., 2017). Its consideration allowed us to design the experiment and interpret the results. Norms and expectations are context specific and are unconsciously activated by situational cues (Cárdenas & Ostrom, 2004; Krupka & Weber, 2013; Bouma & Ansink, 2013). Framing increased subjects' familiarity with the task providing the situational cues for each fishing context as suggested by the differences between treatments in high-performance associations. Our study also contributes to the literature supporting the external validity of lab-in-the-field experiments because performance under CEAR in real life correlated to the stewardship displayed in the game (Rustagi et al., 2010; Carpenter & Seki, 2011; Gelcich et al., 2013; Basurto et al., 2016).

The interpretation that access regimes drive the differences between frames should be made with caution. Access regimes are not the only difference between the loco and the hake fishery. Loco is harvested by diving, whereas hake is fished using gill nets and longlines. The loco fishery collapsed in the 1980s. After its transition to the TURF system, its status has improved (Gelcich et al., 2010). Instead, the hake fishery started its decline in the early 2000s and its status is still unstable (Arancibia & Neira, 2008; Plotnek et al., 2016). Differences like these can affect the mental models that drive decisions under each fishing context (Gelcich et al., 2007). Yet, the fact that the differences between frames occurred only in high-performance associations indicates that access regimes explain the framing effect, at least in part. All associations in our sample share the same historical, biological, and regulatory backgrounds for each of the fisheries (Arancibia & Neira, 2008; Gelcich et al., 2010; Phillips & Pérez-Ramírez, 2017). Arguably, the only difference between high- and low-performance associations was their ability to self-organize under CEAR. If characteristics other than the access regime were driving the differences between the treatments, we would have observed the same patterns of behavior in both types of associations.

The implementation of formal CEARs is a promising approach to respond to the current call for a sustainable and equitable blue economy (Bennett et al., 2019). In our study, fishers from the same association behaved differently when randomly assigned to CPR games signaling different access regimes that they face in real life. This design accounts for the possibility that differences in behavior are only due to subjects' predispositions for collective action, suggesting that CEAR policies can shape users' stewardship. Access regimes seem to shape norms and expectations, but not in all users' groups operating under CEAR. This stresses the need to further identify the conditions under which access policies lead to group dynamics that favor resource stewardship. This knowledge is crucial to guide the design of access regimes that promote the sustainable use of CPRs.

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LITERATURE CITED

Alekseev, A., Charness, G., & Gneezy, U. (2017). Experimental methods: When and why contextual instructions are important. *Journal of Economic Behavior & Organization*, *134*, 48–59.

Andreoni J. (1990). Impure altruism and donations to public goods: A theory of warm-glow giving. *The Economic Journal*, *100*, 464–477.

Andreoni, J. (1995). Cooperation in Public-Goods Experiments: Kindness or Confusion?. *The American Economic Review*, *85*(4), 891–904. https://www.jstor.org/stable/2118238

Arancibia, H., & Neira, S. (2008). Overview of the Chilean hake (*Merluccius gayi*) stock, a biomass forecast, and the jumbo squid (*Dosidicus gigas*) predator-prey relationship off central Chile. *California Cooperative Oceanic Fisheries Investigations Report*, *49*, 104–115.

Basurto X., Blanco E., Nenadovic M., Vollan B. (2016). Integrating simultaneous prosocial and antisocial behavior into theories of collective action. *Science Advances*, *2*, e1501220.

Bennett N. J., Cisneros-Montemayor A. M., Blythe J., Silver J. J., Singh G., Andrews N., Calò A., Christie P., Di Franco A., Finkbeiner E. M., Gelcich S., Guidetti P., Harper S., Hotte N., Kittinger J. N., Le Billon P., Lister J., López De La Lama R., Mckinley E., … Sumaila U. R. (2019). Towards a sustainable and equitable blue economy. *Nature Sustainability*, *2*, 991–993.

Bennett N. J., Whitty T. S., Finkbeiner E., Pittman J., Bassett H., Gelcich S., Allison E. H. (2018). Environmental stewardship: A conceptual review and analytical framework. *Environmental Management*, *61*, 597–614.

Bergseth B. J., Russ G. R., Cinner J. E. (2015). Measuring and monitoring compliance in no-take marine reserves. *Fish and Fisheries*, *16*, 240–258.

Bolton G. E., Ockenfels A. (2000). ERC: A theory of equity, reciprocity, and competition. *The American Economic Review*, *90*, 166–193.

Bouma J., Ansink E. (2013). The role of legitimacy perceptions in self-restricted resource use: A framed field experiment. *Forest Policy and Economics*, *37*, 84–93.

Cardenas J. C. (2011). Social norms and behavior in the local commons as seen through the lens of field experiments. *Environmental and Resource Economics*, *48*, 451–485.

Cárdenas J.-C., Ostrom E. (2004). What do people bring into the game? Experiments in the field about cooperation in the commons. *Agricultural Systems*, *82*, 307–326.

Carpenter J., Seki E. (2011). Do social preferences increase productivity? Field experimental evidence from fishermen in Toyama Bay. *Economic Inquiry*, *49*, 612–630.

Chaudhuri A. (2011). Sustaining cooperation in laboratory public goods experiments: A selective survey of the literature. *Experimental Economics*, *14*, 47–83.

Costello C., Ovando D., Hilborn R., Gaines S. D., Deschenes O., & Lester S. E. (2012). Status and solutions for the world's unassessed fisheries. *Science*, *338*, 517–520.

Couto M. C., Pacheco J. M., Santos F. C. (2020). Governance of risky public goods under graduated punishment. *Journal of Theoretical Biology*, *505*, 110423.

Donlan C. J., Wilcox C., Luque G. M., Gelcich S. (2020). Estimating illegal fishing from enforcement officers. *Scientific Reports*, *10*, 1–9.

Dufwenberg M., Gächter S., Hennig-Schmidt H. (2011). The framing of games and the psychology of play. *Games and Economic Behavior*, *73*, 459–478.

Ellingsen T., Johannesson M., Mollerstrom J., Munkhammar S. (2012). Social framing effects: Preferences or beliefs? *Games and Economic Behavior*, *76*, 117–130.

Fehr E., Gächter S. (2000). Fairness and retaliation: The economics of reciprocity. *Journal of Economic Perspectives*, *14*, 159–182.

Fehr E., & Schmidt K. M. (1999). A theory of fairness, competition, and cooperation. *The Quarterly Journal of Economics*, *114*, 817–868.

Fehr E., Schurtenberger I. (2018). Normative foundations of human cooperation. *Nature Human Behaviour*, *2*, 458–468

Fischbacher U. (2007). z-Tree: Zurich toolbox for ready-made economic experiments. *Experimental Economics*, *10*, 171–178.

Gachter S., Renner E., & Sefton M. (2008). The long-run benefits of punishment. *Science*, *322*, 1510–1510.

Gavin M. C., Solomon J. N., Blank S. G. (2010). Measuring and monitoring illegal use of natural resources. *Conservation Biology*, *24*,89–100.

Gelcich S., Hughes T. P., Olsson P., Folke C., Defeo O., Fernandez M., Foale S., Gunderson L. H., Rodriguez-Sickert C., Scheffer M., Steneck R. S., & Castilla J. C. (2010). Navigating transformations in governance of Chilean marine coastal resources. *Proceedings of the National Academy of Sciences*, *107*, 16794–16799.

Gelcich S., Edwards-Jones G., Kaiser M. J. (2007). Heterogeneity in fishers' harvesting decisions under a marine territorial user rights policy. *Ecological Economics*, *61*, 246–254.

Gelcich S., Edwards-Jones G., Kaiser M. J., Castilla J. C. (2006). Co-management policy can reduce resilience in traditionally managed marine ecosystems. *Ecosystems*, *9*, 951–966.

Gelcich S., Guzman R., Rodríguez-Sickert C., Castilla J. C., Cárdenas J. C. (2013). Exploring external validity of common pool resource experiments: Insights from artisanal benthic fisheries in Chile. *Ecology and Society*, *18*, 2. https://doi.org/10.5751/ES-05598-180302

Gelcich S., Martínez-Harms M. J., Tapia-Lewin S., Vasquez-Lavin F., Ruano-Chamorro C. (2019). Comanagement of small-scale fisheries and ecosystem services. *Conservation Letters*, *12*, e12637.

Gilmour P. W., Day R. W., Dwyer P. D. (2012). Using private rights to manage natural resources: Is stewardship linked to ownership? *Ecology and Society*, *17* https://doi.org/10.5751/ES-04770-170301.

Herrmann B., Thoni C., & Gachter S. (2008). Antisocial punishment across societies. *Science*, *319*, 1362–1367.

Jentoft S., Mccay B. J., Wilson D. C. (1998). Social theory and fisheries co-management. *Marine Policy*, *22*, 423–436.

Krupka E. L., Weber R. A. (2013). Identifying social norms using coordination games: Why does dictator game sharing vary? *Journal of the European Economic Association*, *11*, 495–524.

Leibbrandt A., Gneezy U., List J. A. (2013). Rise and fall of competitiveness in individualistic and collectivistic societies. *Proceedings of the National Academy of Sciences*, *110*, 9305–9308.

Marín, A., Gelcich, S., Castilla, J. C., & Berkes, F. (2012). Exploring social capital in Chile's coastal benthic co-management system using a network approach. *Ecology & Society*, *17*. https://doi.org/10.5751/ES-04562-170113

Mcdonald G., Wilson M., Veríssimo D., Twohey R., Clemence M., Apistar D., Box S., Butler P., Cadiz F. C., Campbell S. J., Cox C., Effron M., Gaines S., Jakub R., Mancao R. H., Rojas P. T., Tirona R. S., Vianna G. (2020). Catalyzing sustainable fisheries management through behavior change interventions. *Conservation Biology*, *34*, 1176–1189.

Nguyen Thi Quynh C., Schilizzi S., Hailu A., Iftekhar S. (2017). Territorial Use Rights for Fisheries (TURFs): State of the art and the road ahead. *Marine Policy*, *75*, 41–52.

Ostrom, E. (1990). *Governing the commons: The evolution of institutions for collective action*. Cambridge University Press.

Ostrom E. (1998). A behavioral approach to the rational choice theory of collective action: Presidential address, American Political Science Association, 1997. *American Political Science Review*, *92*, 1–22.

Ostrom, E. (2006). The value-added of laboratory experiments for the study of institutions and common-pool resources. *Journal of Economic Behavior & Organization*, *61*, 149–163.

Oyanedel, R., Gelcich, S., & Milner-Gulland, E. J. (2020). Motivations for (non-) compliance with conservation rules by small-scale resource users. *Conservation Letters*, *13*, e12725.

Phillips, B. F., & Pérez-Ramírez, M. (2017). *Climate change impacts on fisheries and aquaculture, 2 volumes: A global analysis*. John Wiley & Sons.

Plotnek, E., Paredes, F., Galvez, M., & Pérez-Ramírez, M. (2016). From unsustainability to MSC certification: A case study of the artisanal Chilean South Pacific hake fishery. *Reviews in Fisheries Science & Aquaculture*, *24*, 230–243.

Rabin, M. (1993). Incorporating fairness into game theory and economics. *The American Economic Review*, *83*, 1281–1302.

Rustagi D., Engel S., & Kosfeld M. (2010). Conditional cooperation and costly monitoring explain success in forest commons management. *Science*, *330*, 961–965.

Schlager E., Ostrom E. (1992). Property-rights regimes and natural resources: A conceptual analysis. *Land Economics*, *68*, 249–262.

Smith, V. (1982). Microeconomic systems as an experimental science. *The American Economic Review*, *72*, 923–955.

Van Putten I., Boschetti F., Fulton E. A., Smith A. D. M., Thebaud O. (2014). Individual transferable quota contribution to environmental stewardship: A theory in need of validation. *Ecology and Society*, *19*. https://doi.org/10.5751/ES-06466-190235.

Vespa E. (2020). An experimental investigation of cooperation in the dynamic common pool game. *International Economic Review*, *61*, 417–440.

Wilen J. E., Cancino J., Uchida H. (2012). The economics of territorial use rights fisheries, or TURFs. *Review of Environmental Economics and Policy*, *6*, 237–257.

Wright G. D., Andersson K. P., Gibson C. C., Evans T. P. (2016). Decentralization can help reduce deforestation when user groups engage with local government. *Proceedings of the National Academy of Sciences*, *113*, 14958–14963.

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

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