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Facultad de Gobierno
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**PSICOBIOLOGÍA DE LA SOCIOSEXUALIDAD EN HOMBRES. UNA
APROXIMACIÓN DESDE LA PSICOMETRÍA Y LA TEORÍA DE JUEGOS**

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I. RESUMEN

El presente trabajo buscó comprender las estrategias reproductivas en los hombres, integrando aspectos biológicos, psicológicos y conductuales en un marco evolutivo. Se presentan dos manuscritos publicados: “The Male Warrior Hypothesis: Testosterone-related Cooperation and Aggression in the Context of Intergroup Conflict” y “Testing strategic pluralism: The roles of attractiveness and competitive abilities to understand conditionality in men's short-term reproductive strategies”. El primero busca comprender cómo algunos rasgos antropométricos dependientes de testosterona influyen en la cooperación y agresión en diferentes contextos de conflicto intra e intergrupales. La testosterona es una hormona social y se ha establecido su influencia en la competencia intrasexual y el éxito reproductivo en los hombres. El último estudia el papel de los rasgos de atractivo y las habilidades competitivas en las estrategias reproductivas a corto plazo. Con este trabajo estudiamos en una dimensión más específica aquellos aspectos que tienen incidencia tanto en términos intrasexuales como intersexuales, estableciendo que los rasgos de atractivo son más relevantes para el despliegue de estrategias reproductivas en el corto plazo.

ABSTRACT

The present work sought to understand the reproductive strategies in men, integrating biological, psychological, and behavioral aspects in an evolutionary framework. Two published manuscripts are presented: “The Male Warrior Hypothesis: Testosterone-related Cooperation and Aggression in the Context of Intergroup Conflict” and “Testing strategic pluralism: The roles of attractiveness and competitive abilities to understand conditionality in men's short-term reproductive strategies”. The first one seeks to understand how some testosterone-dependent anthropometric traits influence cooperation and aggression in different contexts of intra- and intergroup conflict. Testosterone is a social hormone and its influence on intrasexual competition and reproductive success in men has been established. The later studies the role of attractiveness traits and competitive abilities on short-term reproductive strategies. With this work we study in a more specific dimension those aspects that have an incidence both in intrasexual and intersexual terms, establishing that attractiveness traits are more relevant for the deployment of reproductive strategies in the short term.

II. INTRODUCCIÓN

Las estrategias reproductivas constituyen conjuntos integrados de adaptaciones relacionadas con la inversión de tiempo y energía en los diferentes eventos reproductivos. En este sentido, la hipótesis del pluralismo estratégico otorga una explicación evolutiva a la manera en la que se gestiona el *trade-off* entre la inversión en apareamiento o en cuidados parentales (Gangestad & Simpson, 2000). Desde ahí, se plantea que ambos sexos han debido desarrollar estrategias específicas, que se van resolviendo en función de los costos de oportunidad que entrega el contexto de cada individuo. Así, para las mujeres el desafío es atraer y retener a un compañero que sea poseedor de buenos genes y a la vez, sea un buen proveedor de recursos para la descendencia. Sin embargo, encontrar ambos rasgos en un mismo individuo es complejo y, a su vez, no todas las mujeres cuentan con las características necesarias para atraer y retener a un compañero con ambas particularidades en una relación de largo plazo (Gangestad & Simpson, 2000; Schmitt & Buss, 2018). En este sentido, la estrategia para las mujeres estaría dada por buscar en una pareja a alguien que sea capaz de proveer recursos a largo plazo y por otro lado, en una relación extra pareja buenos genes para la descendencia (Gangestad & Simpson, 2000). Para los hombres, la estrategia ideal para la resolución de este *trade-off* se encontraría en la inversión de sus recursos en cuidados parentales, pero manteniendo el interés por relaciones extra pareja, con lo que maximizarían su

eficacia biológica, aumentando las posibilidades de tener un mayor número de descendientes (Gangestad & Simpson, 2000; Schmitt & Buss, 2018).

Particularmente en el caso de los hombres la resolución de este *trade-off* es relevante ya que es el sexo que menor inversión parental obligada presenta y por ende es el sexo menos selectivo (Trivers, 1972). No obstante, la inversión parental facultativa del hombre puede ser elevada ya que en determinadas circunstancias es importante para la supervivencia y el desarrollo de una buena condición de la descendencia. También, es el que ha desarrollado mayores habilidades de competencia intrasexual, es decir, la competencia con miembros del mismo sexo por acceso a parejas del sexo opuesto (Buss & Schmitt, 2019). Esto, se traduce en términos psicológicos y comportamentales en el despliegue de una sociosexualidad más o menos restrictiva. La sociosexualidad se ha definido como la predisposición individual a tener relaciones sexuales sin compromiso previo (Simpson & Gangestad, 1991). Así, alguien que tenga una sociosexualidad menos restrictiva tenderá a maximizar el número de parejas sexuales a lo largo de su vida (orientación hacia el corto plazo), mientras que alguien que tenga una sociosexualidad más restrictiva tendrá una preferencia por enfocar sus recursos en los cuidados parentales y mostrará una orientación hacia el largo plazo (Simpson & Gangestad, 1991). En términos metodológicos, la sociosexualidad se mide a partir de la Escala de Orientación Sociosexual, desarrollada por Simpson y Gangestad, en la década del '90. Esta escala, en su versión original consta de 7 ítems (4 preguntas de respuesta abierta y 3 en escala

Likert de 7 puntos) y permite establecer la predisposición a establecer relaciones de corto plazo. Este instrumento, entrega una medida de la sociosexualidad de forma unidimensional ya que no considera la predisposición de los sujetos a comprometerse en relaciones de largo plazo (Jackson & Kirkpatrick, 2007). En una nueva versión del instrumento, Jackson y Kirkpatrick (2007), incluyen nuevos ítems y definen el constructo en términos multidimensionales, es decir, orientación hacia el corto plazo, largo plazo e historia de las relaciones pasadas y en el futuro cercano. Este último estudio permitió ampliar el espectro de información respecto de las estrategias reproductivas en humanos ya que permite visualizar una estrategia a corto y largo plazo en un mismo individuo de forma secuencial o simultánea y además establece una medida de éxito reproductivo (Jackson & Kirkpatrick, 2007).

Otro de los fenómenos que contribuyen a la supervivencia y al éxito reproductivo son los mecanismos de cooperación, los que han evolucionado facilitando la adaptación al ambiente, ya que proporciona el acceso a recursos, pero que también han generado otros desafíos que influyen en la organización social (Aguirre- Dávila, 2011; Rand & Nowak, 2013). La cooperación se define como cualquier acto que otorga un beneficio a otro, pero que no necesariamente beneficia al individuo en términos personales ni contingentes (Rand & Nowak, 2013). Para entender cómo y en qué contextos opera la cooperación se han propuesto distintos modelos que habrían evolucionado de manera específica y que van desde la reciprocidad directa, hasta aquellos que requieren de variables

contextuales como la reputación, el espacio geográfico y el parentesco (Barclay & Van Vugt, 2015). A este respecto, el conflicto con grupos rivales ha jugado un papel fundamental en la aparición y evolución de la cooperación intragrupo (McDonald, Navarrete, & Van Vugt, 2012). En este sentido, la hipótesis del macho guerrero explica en términos evolutivos como es que los seres humanos han resuelto los conflictos fuera del grupo –como ocurre en una situación de guerra– señalando que, “los humanos, particularmente los hombres, podrían poseer mecanismos psicológicos que les permitan formar coaliciones capaces de planificar, iniciar y ejecutar actos de agresión en miembros de grupos externos, con el objetivo final de proteger los recursos del grupo” (McDonald et al., 2012, p. 671). Por otro lado, el participar en conflictos fuera del grupo, influye en el éxito reproductivo de los hombres ya que esto aumenta su estatus, haciendo al individuo más elegible en términos de selección intersexual (Buss & Schmitt, 2019; McDonald et al., 2012).

Otro de los componentes importantes en torno a la adquisición de estatus tiene que ver con el atractivo físico. A partir de la década del '70 se comienza a investigar acerca de la influencia de ciertos rasgos que denotan atractivo, a partir del estudio de Dion, Berscheid, & Walster (1972), desde donde se establece que los seres humanos tienen una tendencia natural y universal a atribuir características positivas a aquello que les parece atractivo. Además, se ha establecido que las personas que son consideradas como atractivas son menos sancionadas en multas de tráfico y acceden a mejores posiciones laborales. Los

hombres que son más atractivos, poseen una ventaja en términos de selección intersexual, ya que el atractivo físico se ha asociado a una buena calidad genética, lo que es valorado por las mujeres a la hora de elegir pareja (Buss & Schmitt, 2019). En este sentido, se ha establecido que existen ciertos rasgos físicos que se han asociado con el atractivo. Una de estas medidas es la asimetría fluctuante facial, que se entiende como un indicador de estabilidad genética en el desarrollo de un individuo pese a la interacción con el medio ambiente (Kordsmeyer & Penke, 2017). Así, se ha establecido que los hombres menos asimétricos son considerados como más atractivos, menos fieles y se ha asociado una tendencia a mostrar una sociosexualidad menos restrictiva, por ende tienen un mayor número de parejas sexuales (Thornhill & Gangestad, 1994). Otro rasgo considerado como atractivo es la fuerza, ya que, además de ser relevante a la hora de competir intrasexualmente por el acceso a parejas, también es un rasgo indicador de la capacidad de competir y acaparar otro tipo de recursos, y se ha visto que tiene un efecto sobre las estrategias reproductivas a corto plazo (Kordsmeyer, Hunt, Puts, Ostner, & Penke, 2018; Lukaszewski, Larson, Gildersleeve, Roney, & Haselton, 2014). Por otro lado, las habilidades de lucha se han asociado a la adquisición de estatus dentro del grupo y también como una característica importante en términos de competencia intrasexual (Muñoz-Reyes, Gil-Burmann, Fink, & Turiegano, 2012). En términos reproductivos las habilidades de lucha se asocian de manera directa con la competencia intrasexual, es decir, aquellos sujetos con mayores habilidades de

lucha probablemente se configuren como dominantes entre su grupo de pares adquiriendo una ventaja por sobre el resto a la hora de elegir y retener a una pareja (Muñoz-Reyes et al., 2012).

A nivel fisiológico, tanto los rasgos de atractivo como las habilidades de lucha se encuentran moduladas por la testosterona. La testosterona es una hormona androgenizante que tiene efectos a nivel organizacional (en la etapa prenatal y en la pubertad) y activacional. En términos morfológicos, una de las medidas del efecto de esta hormona a nivel prenatal es el índice 2D:4D, que corresponde a la longitud de los dedos de las manos del segundo y cuarto dedo. Existen estudios que han encontrado asociación de este índice con el despliegue de comportamientos agresivos (Bailey & Hurd, 2005). A su vez, Van Honk, Montoya, Bos, Van Vugt, & Terburg (2012), encuentran un efecto de la exposición a testosterona prenatal baja o alta con la cooperación, estableciendo que los sujetos con baja exposición a la hormona contribuyeron más al grupo en condiciones experimentales en comparación a quienes tenían una alta exposición durante la etapa prenatal en un juego de bienes públicos. A nivel puberal, la testosterona tiene un rol en la aparición de las características sexuales secundarias. Uno de los marcadores antropométricos de la exposición a testosterona es la masculinización facial. En este sentido, aquellos individuos con una mayor masculinidad facial tienden a considerarse y ser considerados como poseedores de mayores habilidades de lucha, más competitivos, más agresivos y menos confiables (Edelstein, Chopik, & Kean, 2011; Edwards, 2006; Gangestad

& Simpson, 2000; Muñoz-Reyes et al., 2012; Oliveira et al., 2014; Sanchez-Pages & Turiegano, 2010; Schacht & Borgerhoff Mulder, 2015). Estos resultados, han sido respaldados por evidencia comportamental que apunta a una asociación positiva entre masculinidad facial y la frecuencia e intensidad de la agresión (Carré, McCormick, & Hariri, 2011). A su vez, la masculinidad facial se asocia a un mayor número de parejas sexuales (Arnocky, Woodruff, & Schmitt, 2016), y también ha sido vinculada positivamente con una mayor tendencia a buscar relaciones de corto plazo (Boothroyd, Jones, Burt, DeBruine, & Perrett, 2008; Kruger, 2006). Además se ha visto que hombres que poseen una masculinidad facial y masa muscular por encima del promedio, muestran una tendencia mayor a establecer relaciones de corto plazo y también tienen mayor éxito reproductivo, lo que es coherente con una estrategia de corto plazo (Polo, Muñoz-Reyes, Pita, Shackelford, & Fink, 2019). Sin embargo, se ha encontrado que en términos intersexuales las mujeres prefieren rostros masculinos promedio, lo que de alguna manera compensaría el trade off entre buenos genes y cuidados parentales (Ekrami et al., 2020).

A partir de la necesidad de generar evidencia para el campo, es que en esta investigación se ha estudiado cómo es que la sociosexualidad podría estar relacionada con distintos comportamientos que se observan en la especie humana, integrando aspectos biológicos, psicológicos y comportamentales. Por ello, en el primer manuscrito “The Male Warrior Hypothesis: Testosterone-related Cooperation and Aggression in the Context of Intergroup Conflict”, se estudia el

rol de la testosterona a partir de indicadores antropométricos de exposición a esta hormona en la etapa prenatal (medido a partir del índice 2D:4D) y en la etapa puberal (medido a partir de la masculinización facial y la musculatura corporal) tanto en la cooperación como en la agresión en contextos experimentales de conflicto intergrupo. Esto, en términos de estrategias reproductivas tiene incidencia en el éxito reproductivo y en el despliegue de estrategias de competencia intrasexual. Por otra parte, el segundo manuscrito "Testing strategic pluralism: The roles of attractiveness and competitive abilities to understand conditionality in men's short-term reproductive strategies", buscó estudiar de forma específica cómo es que los rasgos biológicos y psicológicos de atractivo físico (medidos como asimetría fluctuante y autopercepción de atractivo) y habilidades de lucha (medidos como la testosterona basal y la autopercepción de habilidades de lucha) podrían estar afectando la sociosexualidad a corto plazo en hombres. En esta investigación el principal resultado apunta a la importancia del atractivo físico para el despliegue de una sociosexualidad no restrictiva. Ambas investigaciones se enmarcan en el campo de estudio del despliegue de estrategias reproductivas en hombres y sus implicancias en otros comportamientos inter e intrasexuales, considerando para ello el estudio interdisciplinario e integrado del comportamiento humano.

En cuanto a las implicancias de este trabajo hacia problemáticas sociales la hipótesis del macho guerrero permite entender cómo es que se generan interacciones en grupos que son diferentes y además permite entender porque

aparecen las conductas de agresión entre grupos y a su vez de cooperación intragrupal. Por otro lado, otorga información en torno a las diferencias sexuales en la expresión de la agresión en situaciones de conflicto intergrupal, donde el grupo externo se percibe como amenazante, tal como ocurre con el fenómeno de la migración (McDonald et al., 2012). Para el caso particular de la migración, la hipótesis del macho guerrero propone facilitar interacciones positivas entre hombres, ya que son ellos el principal foco de agresión en las interacciones intergrupales. Con esto, se busca disminuir las percepciones de amenaza que fomentan la aparición de conductas xenófobas. Por ejemplo, en la década del '70 en EE.UU se realizaron una serie de experimentos para aplacar el conflicto racial en colegios, donde a partir del aprendizaje colaborativo se propiciaron interacciones positivas y se manipuló el contexto para disminuir las diferencias de estatus entre estudiantes, lo que tuvo un impacto positivo en la autoestima y el rendimiento académico (Aronson & Bridgeman, 1979) . Por otro lado, el estudio integrado de variables que influyen directamente en el éxito reproductivo de los sujetos permite robustecer la comprensión de uno de los hitos más relevantes en la ontogenia de un individuo, como es la búsqueda y elección de una pareja. A partir de esta comprensión, podemos caracterizar de mejor forma las dinámicas sociales inter e intrasexuales que surgen de este proceso y, de esta forma, abordar problemas de alta relevancia asociados a este, y que se pueden expresar en ámbitos tan distintos como el mercado laboral o la convivencia escolar.

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The Male Warrior Hypothesis: Testosterone-related Cooperation and Aggression in the Context of Intergroup Conflict

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The Male Warrior Hypothesis (MWH) establishes that men's psychology has been shaped by inter-group competition to acquire and protect reproductive resources. In this context, sex-specific selective pressures would have favored cooperation with the members of one's group in combination with hostility towards outsiders. We investigate the role of developmental testosterone, as measured indirectly through static markers of prenatal testosterone (2D:4D digit ratio) and pubertal testosterone (body musculature and facial masculinity), on both cooperation and aggressive behavior in the context of intergroup conflict among men. Supporting the MWH, our results show that the intergroup conflict scenario promotes cooperation within group members and aggression toward outgroup members. Regarding the hormonal underpinnings of this phenomenon, we find that body musculature is positively associated with aggression and cooperation, but only for cooperation when context (intergroup competition) is taken into account. Finally, we did not find evidence that the formidability of the group affected individual rates of aggression or cooperation, controlling for individual characteristics.

Human beings are adapted to living in social groups. This pattern of behavior has shaped the evolution of the human mind, favoring behavioral strategies that benefit group formation and cohesion through cooperation with non-genetically related individuals¹. Living in groups provides enormous benefits in relation to hunting and protection against predators, but also creates scenarios of inter-group conflict. Moreover, it has been argued that intra-group cooperation co-evolved with hostility towards outsiders^{2,3}.

Archaeological and comparative evidence indicates that inter-group conflict has been present since the dawn of our lineage⁴. Anthropological studies of tribal societies in the 20th and 21st centuries have shed light on the benefits of inter-group conflict for males⁵, shaped by sexual selection to compete through physical aggression^{6,7}. The male warrior hypothesis argues that “humans, particularly men, may possess psychological mechanisms enabling them to form coalitions capable of planning, initiating and executing acts of aggression on members of outgroups, with the ultimate goal of acquiring or protecting reproductive resources”⁸. In this context, testosterone has been shown to play an important role in cooperative and aggressive behaviors, functioning as a status-seeking hormone⁹. However, little research has been done on the effect of this hormone on levels of aggression and cooperation in the context of intergroup conflict among men.

The male warrior hypothesis is a sex-specific proposal primarily supported theoretically by the greater degree of variance among men than among women in terms of reproductive success^{10,11} and the lower level of obligatory parental investment by men¹². These two factors have enhanced intrasexual competition in men, thus favoring sexual dimorphism in size and strength, accompanied by a significant sex-based difference in physical aggressiveness⁶. In this sense, men have enormous incentives to form coalitions to be involved in intergroup contests because of the benefits associated with winning these contests, even if the costs of losing the contest could be devastating¹³. Therefore, in contrast to women, men can exacerbate intra-group cooperation¹⁴ and intergroup

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aggression¹⁵ in the context of an intergroup threat, the most important factor triggering these behaviors being the incentives to monopolize resources. Moreover, exacerbation of intergroup conflict in men can lead to the expression of spiteful behaviors in which participants prefer to inflict damage to themselves at the expense of inflicting much greater damage to individuals of a competing group¹⁵.

Aggression and cooperation are multifactorial phenomena that are ubiquitous to human societies. Although aggression and cooperation seem to be opposite behaviors, they have several aspects in common. Both are generally employed to resolve conflicts over access to limited resources and social status. Therefore, they are important for success in mating^{6,15–17}. Aggression can be considered a mechanism of intrasexual competition through peer domination^{6,15,18,19}. In fact, the literature shows positive relationships between aggressiveness with dating²⁰ and sexual activity²¹ in adolescents. In contrast, cooperation is a costly and honest signal of an individual's ability to obtain a great amount of resources²², which allows him to share them with his peers for the benefit of the group. As a result, the cooperative individual is perceived as a valuable and resourceful ally, which in turn enhances the prestige and status of cooperative individuals^{17,23}, increasing their mating opportunities. Accordingly, both behaviors are related to social status and reproductive success, although through different behavioral pathways²⁴. In addition, in the specific context of intergroup conflict, cooperation and aggression are inevitable interdependent behaviors as men cooperate and form coalitions to outcompete other groups, or in other words, they cooperate to aggress.

Aggression and cooperation are affected by hormones, particularly by testosterone in males^{9,25}. Testosterone (T) is a sex hormone associated with physical and psychological androgenization²⁶. It has been well described that T activates male mating behavior in several species, including humans^{27,28}. However, T is also of special interest in the study of aggression and cooperation because it influences the brain in situations strongly associated with the struggle for status^{9,29}. The effect of T on behavior may be related to three ontogenetic moments: (1) circulating T levels, (2) prenatal T levels, and (3) pubertal T levels. Whereas circulating T levels exert an activation role on behavior, prenatal and pubertal T levels represent the developmental effects of testosterone, exerting an organizing role on the central nervous system, and through this, influencing lifelong behavior^{30,31}. Given the difficulty of carrying out a cohort study, research on the relationship between developmental T levels and current behavior is centered on anthropometric traits, whose expression partly depends on developmental T levels. The length ratio of the second and fourth fingers (2D:4D) is commonly used as an indicator of prenatal T³², while facial masculinization^{33,34} and body muscularity³⁵ are common T indicators of pubertal T.

Prenatal T levels are positively associated with aggressive dispositions, although the magnitude of the effect seems to be small^{36,37}. Only two studies have investigated this relationship in the specific context of intergroup competition, and both had mixed results. McIntyre *et al.*³⁸ used a war game in which participants played the role of the leader of a country in conflict with a neighbor over newly discovered diamond mines on disputed territory. The authors demonstrated that men with lower 2D:4D ratios (higher prenatal T) were more prone to make unprovoked attacks during the course of the game. In contrast, in a recent study, Isbell³⁹ did not find any difference in 2D:4D according to decisions taken when subjects interact with teammates or rivals in the ultimatum game. Similarly, pubertal T levels, as assessed through cues like facial masculinity and muscularity through strength, have been shown to be positively associated with aggression^{40,41}. In the specific context of intergroup competition, masculine faces are associated with wartime leadership⁴². Moreover, there is cross-cultural evidence supporting a positive association between body strength and the tendency to be more supportive of military action⁴³, a proxy of the propensity to engage in serious intergroup conflict.

Prenatal T levels have also been shown to be positively associated with higher levels of cooperative behavior in a social dilemma and more generous offers in the dictator game⁴⁴. However, the relationship between prenatal T levels and behavior was the reverse when aggressive cues were presented before participants began playing⁴⁴, suggesting an important role of context in triggering cooperative or aggressive behavior. In general, the effect of 2D:4D on cooperative behavior is not consistent across studies. Studies have found that intermediate 2D:4D ratios are related to cooperative behavior in the prisoner's dilemma and dictator games^{45,46}. Millet and Dewitte⁴⁷ investigated the effect of 2D:4D on contributions in a public good game (PGG) and found that individuals with lower 2D:4D ratios make minimal contributions to reaching the provision point (the threshold at which the public good is distributed among the players), considering equal contributions by all players, but neither less (selfish behavior) nor more (altruistic behavior). Less conclusive evidence has been reported concerning the role of pubertal T levels on cooperative behavior. First, studies have failed to show a relationship between facial masculinity and cooperation as assessed in the PGG⁴⁸ or with the social value inventory⁴⁹. Another study found that more muscular men were less oriented to egalitarianism⁵⁰, that is, favoring equal benefits among group members. However, Stirrat & Perret¹⁹ found that facial masculinity is a positive predictor of cooperative behavior in PGG, but only in the context of intergroup competition. When participants play a PGG without the threat of another group, the relationship among traits is negative¹⁹. This suggests that the intergroup context is a key aspect in evaluating the effect of pubertal T on cooperation.

Another key prediction arising from The male warrior hypothesis is the effect of group formidability on the expression of both aggressive and cooperative behavior in the presence of an intergroup threat⁸. Individuals tend to assess group formidability from the overall body musculature of the outgroup⁵¹ and from the presence or absence of a successful outgroup leader⁵². Similar to the finding that more formidable individuals tend to behave more aggressively when facing a conflict⁵³, it can be expected that individual behavior during intergroup conflict is influenced by group formidability⁵². In this sense, group formidability influences the likelihood of an escalating conflict in sports⁵⁴.

The evidence reported in the paragraphs above indicates that developmental T, especially in the context of intergroup conflict, plays a key role in influencing behavioral changes related to cooperation and aggression, as predicted by the male warrior hypothesis. However, as far as we have been able to determine, there have been no studies that measure the three effects of developmental T on aggression and cooperation in intergroup conflict

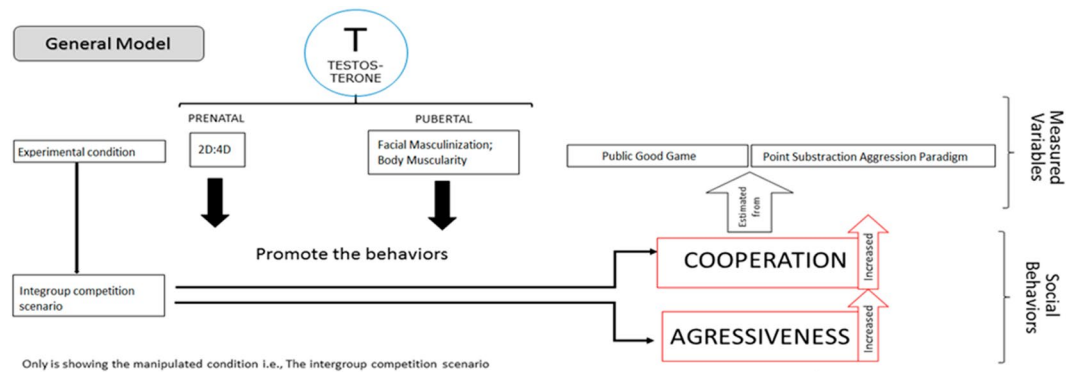


Figure 1. General research model.

scenarios versus control conditions. This is important since T levels during developmental stages, especially during puberty, influence traits linked to physical strength, like skeletal muscle mass (SMM), which affect different behavioral manifestations^{53,55}. Moreover, traits related to developmental T levels are thought to play an important role in intrasexual competition⁵⁶ and, consequently, in intergroup conflict. In the present study, we used an experimental design to assess differences in aggression and cooperation based respectively on Cherek's Point Subtraction Aggression Paradigm (PSAP)⁵⁷ and a Public Good Game (PGG) under two conditions: intergroup conflict (21 groups of 6 individuals each), and a control condition in which the outgroup threat was removed (20 groups). We measured: (1) prenatal T levels (from 2D:4D), and (2) pubertal T levels (from facial width-to-height ratio, and body muscularity). Our predictions were as follow (Fig. 1):

- First, using a larger sample and a new population, we expect to replicate the previous results that indicate that intra-group cooperation and inter-group aggression are heightened in the context of intergroup conflict.
- Second, the use of aggression among human males is related to T-dependent physical traits. We expect this relationship to be positive in the contexts of both dyadic (one-to-one standard PSAP) and inter-group conflict. Accordingly, we expect a positive relationship between developmental T and aggressive behavior in the PSAP task under the control condition and in the context of intergroup competition.
- Third, similar to aggression, the use of cooperation is related to physical T-dependent traits, but in the opposite direction according to the context. More concretely, we expect a positive relationship between developmental T levels and cooperation in the intergroup conflict context, but a negative one in the control context, as previously reported¹⁹.
- Finally, we predict that individuals in more formidable groups, measured as the sum of group muscle mass or as the muscle mass of the most muscular individual in the group (the potential leader), show higher levels of aggression and cooperation than individuals in less formidable groups, but only in the intergroup competition context.

Methods

Participants. Over two years, 246 young men (mean = 22.21 years, standard deviation = 3.20) from public universities in the 5th Region of Chile were recruited. Individuals were usually recruited as a group of 6 members who therefore knew each other. Four individuals were excluded because they did not complete the participation in all the games. We chose young adults because intrasexual competition and aggression are more intense in that period of life⁵⁸. At the end of the experimental protocol, participants received \$15,000 Chilean pesos each (around \$23 USD) for participating. They received an additional payment of up to another \$15,000 pesos according to their performance in the games. Thus, participants could receive a maximum of \$30,000 pesos, and in fact, 90% of the participants received that amount. We decided to give a significant amount of money (\$30,000 pesos represents 10% of the minimum monthly wage in Chile) to ensure interest and reliable participation.

Ethics committee authorization and ensuring anonymity. The Institutional Bioethics Committee of the Universidad de Playa Ancha approved the research, including protocols and data treatment. All methods were performed in accordance with the relevant guidelines and regulations. Participants were asked to read and sign an informed consent form that detailed the procedure and the confidentiality steps. We used a standard coding process to preserve the anonymity of the participants^{18,59}. All the participants signed the informed consent prior to their participation in the study.

Group formation, context manipulation, and the data collection procedure. Each group of 6 participants was randomly assigned to one of two treatments, an experimental condition in which the intergroup competition scenario was presented, and a control condition in which no mention was made about an intergroup threat. There were 20 groups of each condition. More details of the conditions of the games are provided below. The games were conducted in the Laboratorio de Comportamiento Animal y Humano (www.labcah.cl) of the University of Playa Ancha, Chile. This laboratory has six experimental cabins with computers connected in a local

network. The cabins are isolated from visual and audio stimuli. This ensures a high level of reliability in the performance of games, prevents talking among participants and favors their concentration. The data were taken in two sessions for each group, with one week between sessions. The first day, we applied a sociodemographic questionnaire (i.e. sexual orientation and age), conducted the Public Good Game, and took anthropometric measurements. The next week, participants performed the Point Subtraction Aggression Paradigm and received their payment. Groups were usually composed of individuals who were familiar with one another. However, in a few groups, some individuals did not know each other because they were friends of friends. We statistically controlled this heterogeneity of the group composition in terms of friendship.

Anthropometric measurements. *Indirect measurement of prenatal testosterone.* Digit Ratio (2D:4D). Prenatal testosterone was inferred from measuring right-hand fingers based on earlier studies that indicate that prenatal T is most reliably estimated by this method^{29,60}. We followed the protocol proposed by Manning³², and replicated by Muñoz-Reyes *et al.*⁶¹. We took two measurements of all the fingers and used the mean value from the two measurements. Measurements were obtained from the basal crease of the finger to the tip of the 2nd and 4th fingers. We used a high-precision digital caliper (± 0.01 cm). The resulting variance (SD = 0.001) was similar to that obtained for this index in previous studies SD = 0.03 in^{60,61}, which indicates a good level of precision.

Indirect measure of pubertal testosterone. Facial masculinity. Facial photographs in frontal view were taken of all participants with a digital SLR camera (Nikon D7000) under standardized conditions, in terms of light and head orientation, focal length (3 m), shutter speed (1/60 s) and aperture (*f*/5.6). Any facial adornments were removed, and participants were asked to look straight into the camera with a neutral expression.

Facial masculinity was based on the facial width-to-height ratio (FWHR), which was calculated using the vertical distance between the highest point of the upper lip and the nasion. We also measured facial width using the horizontal distance between the left and right zygion (i.e., bizygomatic width, the maximum horizontal distance between the right and left facial boundaries). Landmarks were located manually with TPS software. Finally, we compared our manual measurements with those obtained by the software FACE++, which locates and returns high precision facial landmarks. We automated the use of this software through an algorithm in MatLab created by the eighth author, which is connected to the Application Programming Interface of FACE++. There was a high degree of correlation between our fWHR measurements and those obtained from the MatLab algorithm ($r = 0.82$). The results were the same with either of the two FWHR measurements. Given the high degree of correlation between these methods, we preferred to use the manual measurements due to their proven utility in previous studies⁶².

Body Muscularity. We followed the protocol used by Muñoz-Reyes *et al.*⁵⁵. We first measured the participants' height in centimeters, barefoot, and with a manual stadiometer (SECA® 203). We then used the InBody® 370 body composition analyzer to estimate muscularity in kilograms. This device uses a tetrapolar 8-point tactile electrode to measure body composition by direct segmental multifrequency bioelectrical impedance analysis (DSM-BIA). This technique divides the body into five cylindrical parts before estimating impedance separately for each part, i.e., the four limbs and the trunk. The InBody® 370 applies three frequencies (5, 50, and 250 kHz) to measure impedance in the five segments. This methodology has been validated to assess body composition^{63,64}. Bosty-Westphal *et al.*⁶³ found that 97% of the variance in total SMM measured by magnetic resonance imaging was explained by SMM measured by DSM-BIA, whereas Ling *et al.*⁶⁴ compared measurements of total lean mass of men measured using DSM-BIA with those obtained from dual energy X-ray absorptiometry, and found an intraclass correlation coefficient of 0.96. In addition, we collected data on the participants' body mass index (BMI).

Behavioral measurements. For the baseline treatment, we use two experimental paradigms: The Point Subtraction Aggression (PSAP) and The Public Good Game (PGG). Whereas the PSAP paradigm has been used to elicit aggressive inclinations at the individual level in the context of dyadic one-against-one interaction, the PGG has been used to elicit cooperative dispositions in the context of a larger group social dilemma. These control conditions produce measurements of both cooperative and aggressive dispositions at the interpersonal level. The experimental conditions: the intergroup PSAP (IPSA) and the intergroup PGG (IPGG) allows us to respectively explore how intergroup conflict modulates intergroup competition and intra-group cooperation. In all games where interaction was necessary with other men other than those in the group (i.e., dyadic and group conditions), participants were informed that they played with real people, although they were playing against a fictitious opponent (i.e., the software of the games).

Measurement of aggression. The Point Subtraction Aggression Paradigm (PSAP). First applied by Cherek in the 80s, the PSAP is a highly reliable tool to estimate aggression, especially in men⁶⁵. It consists of a computer game in which participants play against a fictitious opponent. Individuals are told that the objective of the game is to score the maximum points, which are exchanged for real money at the end of the game. The participant's score is shown in a central monitor. Participants have three behavioral options that cannot be taken simultaneously:

- a) **Gaining points:** Participants gain 1 point by pressing button A 100 times. One point is equal to \$1,000 Chilean pesos
- b) **Aggression:** Participants are informed that they can steal points from the other participant, but without gaining these points. Therefore, by pressing button B 10 times, they harm their adversary by subtracting one point, but without a concomitant increase in their own point total (i.e., stealing decreases the other player's score without increasing one's own). In addition, participants are told that their rivals get the points that are taken from them. To the extent that the only effect of stealing is to harm your opponent, stealing is consistent with the definition of aggression by Baron and Richardson⁶⁶.

- c) **Protection:** Participants are told that their rivals can steal their points. Participants can avoid losing points by pressing button C 10 times, which protects them from points being subtracted in possible attacks during a fixed period of time.

We conducted a single 10-minute round. Participants under the control condition played the classic dyadic one-against-one version of the PSAP, while the participants under the experimental condition were told that they were part of a group competing with another group in a laboratory of another university located in the capital of the country. They were informed that each one was going to be paired with only one member of the competitor group, but that the winner would be the group that gained more points. The winning group would receive a bonus, equal to the points obtained by the losing group. This bonus would be split evenly between the members of the winning group. The losing group would only receive their individual points. Because the competitor group was fictitious, we always informed the participants that they had won the match, and gave them a bonus equal to 50% of the points obtained by themselves. To achieve more ecological validity and take into account the relevance of aggression in intergroup competition, but also for intragroup status, we followed the strategy used by Geniole *et al.*⁶⁵. In this version, men are provoked intensely (i.e., participants lose 20 points per session). Aggression was calculated as the number of times button B was pressed as a percentage of the total number of times all the buttons were pressed. It is important to note that in our intergroup condition, conflict involves an outgroup threat with real potential consequences in terms of monetary payoffs, which the members of the group can collect by outcompeting the fictitious outgroup. We refer to this version of the PSAP as the Intergroupal PSAP (IPSAP).

Measurement of Cooperation. The public good game. As in any social dilemma, cooperating (any positive contribution) is a dominated strategy (i.e., a strategy that a selfish agent would never implement), but the absence of cooperation leads to an inefficient social outcome. Accordingly, the contributions of individuals can be used to assess their cooperative tendencies⁶⁷. In the present research, we applied the protocol used by Van Vugt *et al.*¹⁴ and replicated by Stirrat & Perrett¹⁹ to measure changes in cooperation with the presence of intergroup conflict in the experimental condition. The public good game was played on computers using z-Tree software⁶⁸.

Participants started the game with \$5,000 Chilean pesos. They could decide how much to invest for the benefit of the group. They were told that they would receive a bonus of \$11,000 pesos when total investment by the group exceeded \$18,000 pesos, regardless of their individual contribution. However, no bonuses would be given if the group failed to contribute more than \$18,000, and participants only gained the amount of money they decided not to share. Under experimental conditions, a group competed with another group for the bonus. As stated before, in the experimental procedure, the rival group was fictitious, although participants were informed that they played against a real group. The group of participants won the PGG if they contributed more than \$18,000. Following previous research^{14,19}, before playing the public good game, participants were provided with a complete description of the game and played a practice game. As part of a wider study, participants played two rounds of the game. The second round of the game was designed to study changes in contributions after winning or losing the first round. This was not included in this study as we were interested in the effect of the intergroup conflict in a one-shot cooperation. The difference between the design of Van Vugt *et al.* and ours is that, as in the IPSAP experimental condition, the outgroup threat involves real monetary consequences. In contrast, the strategy of Van Vugt *et al.* was that the introduction of intergroup conflict relies on priming inter-group competition. Specifically, PGG participants in the PGG from Southampton were told that the study was running simultaneously at 10 different universities in England.

To facilitate the interpretation of our results, let us discuss how the presence of inter-group conflict modifies the incentive structure that subjects face under the IPGG and the IPSAS experimental conditions. The only thing members of the group can do in the IPGG to outcompete other groups, and thus capture the winning prize, is increase intra-group cooperation. Alternatively, under the IPSAP scenario, besides continuing to gain points or defend against potential attacks (intra-group cooperation), stealing points from their opponents (inter-group aggression) also increases the likelihood of outcompeting their opponents.

Data analyses. We conducted two t-tests with independent samples to test our first prediction by comparing mean rates of aggression and contribution according to whether individuals belonged to control or experimental groups. We also employed non-parametric Mann-Whitney U tests because rates of aggression and contribution in the PGG are non-normally distributed variables.

To test our second prediction, we fitted a general linear mixed model (GLMM) considering the following predictor variables: context (i.e., experimental or control), age, 2D:4D ratio, the facial width-to-height ratio, muscle mass, and body mass index. The rate of aggression in the PSAP was our outcome variable.

The third prediction was tested by a GLMM fitted to consider the following predictor variables: context (i.e., experimental or control), age, 2D:4D ratio, the facial width-to-height ratio, muscle mass, and body mass index. The outcome variable was the contribution. We expected an interaction between context and traits that denotes developmental T levels, and we took into account the interaction terms involving these variables.

To test our fourth prediction, we took the fitted model obtained for predictions 2 and 3 and tested whether the interaction of group formidability and context is significant. This assessed the potential effect of group formidability on individual expression of aggression and cooperation in a context of outgroup threat.

We used GLMMs to take into account the hierarchical nature of our data, in which we have individuals in groups and variables at the individual (e.g., muscle mass) and group levels (e.g., group formidability). We employed a step-up strategy to fit our models. In this procedure, all the predictor variables and the predicted interactions were compared individually with the null model. The variable that showed the best fit was introduced in the model. Next, we introduced the remaining variables one-by-one and compared their fit with the previous model (i.e., the reduced model). This procedure continued until no variables improved the reduced model. To compare nested models, we used the Akaike information criterion and the maximum likelihood estimation^{69,70}.

Predictor	Control (N = 119)		Intergroup conflict (N = 123)		t-ratio	p-value
	Mean	SD	Mean	SD		
Age	22.00	3.03	22.37	3.37	-0.908	0.365
SMM	31.86	3.90	31.69	4.28	0.326	0.744
fWHR	2.19	0.18	2.20	0.20	-0.672	0.502
2D:4D	0.952	0.031	0.947	0.027	1.211	0.227
BMI	24.95	3.46	24.79	4.40	-0.270	0.788
Group formidability (Sum SMM)	192.02	10.13	190.14	11.63	-0.550	0.585
Group formidability (Max. SMM)	37.81	3.51	36.82	3.02	-0.970	0.338
Outcome						
Aggression	4.00	4.56	8.25	6.80	-5.689	<0.001
Cooperation	3327.34	1040.48	3655.66	1065.56	-2.424	0.016

Table 1. Descriptive statistics and t-test for all predictors and outcome variables considered in the study.

	COOP.	AGGR.	SMM	FWHR	2D:4D	AGE	BMI
COOP.		$r = -0.059$ $p = 0.517$	$r = 0.152$ $p = 0.093$	$r = -0.120$ $p = 0.187$	$r = -0.040$ $p = 0.662$	$r = -0.135$ $p = 0.135$	$r = -0.017$ $p = 0.853$
AGGR.	$r = 0.019$ $p = 0.837$		$r = 0.097$ $p = 0.287$	$r = 0.027$ $p = 0.764$	$r = 0.084$ $p = 0.354$	$r = -0.064$ $p = 0.482$	$r = -0.039$ $p = 0.666$
SMM	$r = -0.145$ $p = 0.115$	$r = 0.114$ $p = 0.216$		$r = 0.027$ $p = 0.764$	$r = 0.153$ $p = 0.091$	$r = 0.107$ $p = 0.237$	$r = 0.564$ $p < 0.001$
FWHR	$r = 0.014$ $p = 0.878$	$r = -0.005$ $p = 0.959$	$r = 0.208$ $p = 0.023$		$r = 0.181$ $p = 0.046$	$r = -0.094$ $p = 0.301$	$r = 0.197$ $p = 0.029$
2D:4D	$r = -0.168$ $p = 0.068$	$r = 0.066$ $p = 0.473$	$r = -0.107$ $p = 0.248$	$r = -0.016$ $p = 0.859$		$r = 0.172$ $p = 0.056$	$r = 0.151$ $p = 0.095$
AGE	$r = -0.008$ $p = 0.933$	$r = -0.065$ $p = 0.485$	$r = 0.069$ $p = 0.453$	$r = 0.089$ $p = 0.334$	$r = -0.037$ $p = 0.688$		$r = 0.283$ $p = 0.002$
BMI	$r = -0.042$ $p = 0.651$	$r = 0.061$ $p = 0.513$	$r = 0.565$ $p < 0.001$	$r = 0.344$ $p < 0.001$	$r = -0.026$ $p = 0.782$	$r = 0.226$ $p = 0.013$	

Table 2. Spearman's correlation coefficients between variables considered in this study. Relationships between variables in the intergroup context (N = 123) are shown above the diagonal, and relationships between variables in the control context (N = 119) are shown below the diagonal. Note: Coop.: Contribution in the PGG. Aggr.: Aggression in the PSAP.

We considered SMM and BMI together on the one hand and the facial width-to-height ratio and BMI on the other when fitting the models to control for the effect of BMI on SMM and the facial width-to-height ratio. The model related to the aggressive response in the PSAP showed non-normal residual distributions. We transformed the variable rate of aggression as it was very right-skewed by calculating its square root. This transformation solved the problem of the non-normality of the residual. However, because the fitted models were the same as the original and transformed variables, we show the results with the original variable. We employed the statistical package HLM 7 to perform the GLMMs and the IBM SPSS 21 for the t-tests. The level of significance was set at $\alpha = 0.05$.

Results

Differences in aggression and cooperation according to the competitive context. Table 1 shows the descriptive statistics of the variables used in the study according to the context. Table 2 shows Spearman's correlation coefficients between these variables in the control and experimental contexts.

The results of the t-tests showed differences in aggression between the two contexts in the PSAP ($t = -5.722$, $df = 214.03$, $p < 0.001$). Individuals in the intergroup competitive context showed higher rates of aggression (mean = 0.083, SD = 0.070) than individuals in the control condition (mean = 0.040, SD = 0.046). The results of the non-parametric test point to the same pattern (Mann-Whitney U test: $U = 4335.50$, $n_1 = 119$, $n_2 = 123$, $p < 0.001$). As expected, the rate of aggression in the PSAP correlated negatively with profits (Pearson correlation coefficient: $r = -0.549$, $N = 242$, $p < 0.001$) and consequently, individual profits in the experimental condition (mean = 22.36, SD = 5.92) were lower than in the control condition (mean = 24.80, SD = 5.78) ($t = 3.244$, $df = 240$, $p = 0.001$).

The results of the t-tests showed differences in cooperation during the PGG round according to the context (t-test for independent samples: $t = -2.424$, $df = 240$, $p = 0.016$). Individuals facing an intergroup competitive context contribute on average \$328.3 Chilean pesos more (mean = 3655.66, SD = 1065.56) than individuals in the control condition without the outgroup threat (mean = 3327.34, SD = 1040.48). The results of the non-parametric

Parameter	Estimate	Std. Error	df	t	Wald Z	p
<i>Fixed effect</i>						
Intercept	6.028	2.978	240.3	2.040		0.042
Context = 0	-4.299	1.004	41.3	-4.282		<0.001
SMM	0.240	0.104	236.3	2.294		0.023
BMI	-0.215	0.107	236.9	-2.004		0.046
<i>Covariance parameters</i>						
Intergroup	6.260	2.502	39		91.421	<0.001
Residual	27.314	5.226				

Table 3. Fitted model for the relationship between T developmental traits and aggression. Estimates of fixed effects and covariance parameters. Context: [0 = control condition, 1 = intergroup conflict condition]. SMM: Skeletal muscles mass. BMI: Body mass index.

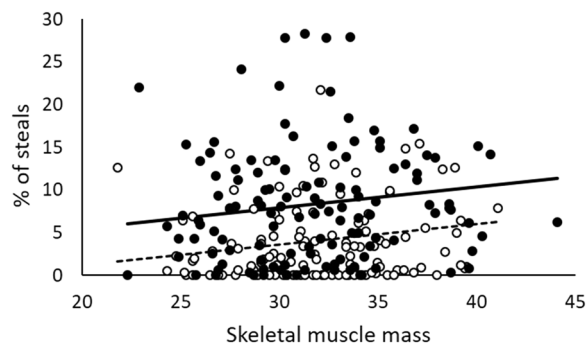


Figure 2. Relationship between skeletal muscle mass and the % of stolen points in the PSAP according to the context. Dots represent observed values in the control (empty dots) and intergroup conflict (full dots) contexts. Lines represent expected values across the observed range for control (slashed line) and intergroup (continuous line) contexts. Expected values are evaluated at the mean value of BMI (24.72).

test point to the same pattern (Mann-Whitney U test: $U = 6153.50$, $n_1 = 119$, $n_2 = 123$, $p = 0.030$). To further explore the effect of context in cooperation, we analyzed cooperation between participants according to whether they invested at least the minimum amount to reach the threshold considering an equal contribution. We found that the effect of context on cooperation was non-linear. Whereas the percentage of individuals that decided to invest \$3,000 pesos or more did not differ between conditions ($X^2 = 0.608$, $df = 1$, $p = 0.435$), the individuals that invested \$3,000 pesos or more in the control condition contributed less (mean = 3719.72, $SD = 673.70$) than those in the experimental condition (mean = 4002.51, $SD = 762.63$) ($t = -2.742$, $df = 194$, $p = 0.007$), but there were no differences among individuals that invested less than 3,000 (control condition: mean = 1852.00, $SD = 832.85$; experimental condition: mean = 1970.95, $SD = 628.66$) ($t = -0.538$, $df = 44$, $p = 0.593$).

We did not find differences between the contexts for any of the predictor variables (see Table 1).

Predictors of aggression in an intergroup conflict scenario. Table 3 shows the fitted model considering prenatal and pubertal markers of T levels according to the context. In addition, we considered age and BMI as control covariables. We found that muscular mass was a positive predictor of aggression in both contexts ($B = 0.238$, $t = 2.294$, $p = 0.023$; see Fig. 2). However, neither the facial width-to-height ratio nor the index 2D:4D were significant predictors of aggression in the PSAP, regardless of the context. We found a main effect of the context ($B = -4.299$, $t = -4.282$, $p < 0.001$). Individuals in the intergroup conflict context were 2.08 times more aggressive than individuals in the control condition when muscular mass and BMI were evaluated in their means (control context: mean = 3.971, $SD = 0.717$; intergroup context: mean = 8.270, $SD = 0.702$). These results further support the previous finding of the effect of context on aggressive behavior.

Predictors of cooperation in an intergroup scenario. Table 4 shows the fitted model considering prenatal and pubertal markers of T levels and their predicted interactions according to context. We also considered age and BMI as control covariables. We found an interaction between context and muscle mass. Muscle mass was negatively related to contributions in the PGG in the control context ($B = -85.633$, $t = -2.624$, $p = 0.009$; see Fig. 3), but positively related in the intergroup conflict context ($B = 50.818$, $t = 2.097$, $p = 0.037$), which partially supports our expectation about the relationship between developmental T levels, context and contribution. Nevertheless, the other traits signaling developmental T levels, the facial width-to-height ratio and the 2D:4D ratio, were not significant predictors of cooperation in either context.

Are aggression and cooperation linked to group formidability? Regarding aggression, we found that the sum of SMM in the group as a measure of group formidability was not related to the number of points

Parameter	Estimate	Std. Error	df	t	Wald Z	p
Fixed effect						
Intercept	2859.83	712.74	242.0	2.012		<0.001
Context=0	2386.89	1045.63	242.0	2.283		0.023
SMM	50.82	24.23	242.0	2.097		0.037
BMI	-32.87	19.90	242.0	-1.652		0.100
Context=0*SMM	-85.63	32.63	242.0	-2.624		0.009
Covariance parameters						
Intergroup	2703.06	51.99	39		35.675	>0.500
Residual	1078787.15	1038.65				

Table 4. Fitted model for the relationship between T developmental traits and cooperation. Estimates of fixed effects and covariance parameters. Context: [0 = control condition, 1 = intergroup conflict condition]. SMM: Skeletal muscles mass. BMI: Body mass index.

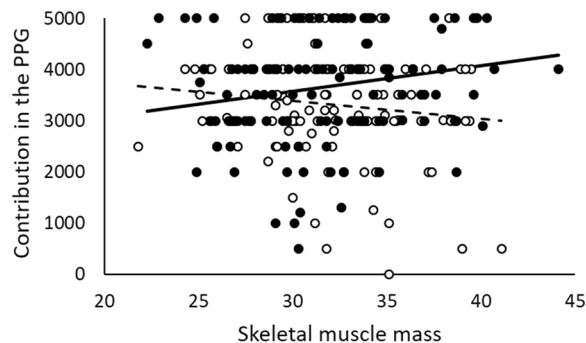


Figure 3. Relationship between skeletal muscle mass and the contribution in the PGG according to the context. Dots represent observed values in the control (empty dots) and intergroup conflict (full dots) contexts. Lines represent expected values across the observed range for control (slashed line) and intergroup (continuous line) contexts. Expected values are evaluated at the mean value of BMI (24.72).

subtracted in the PSAP, either as a main effect ($B = -0.049$, $t = -1.002$, $p = 0.321$) or in interaction with the context ($B = 0.115$, $t = 1.239$, $p = 0.222$). Similar results were found using the maximum individual SMM of the group as a measure of group formidability regarding main effects ($B = -0.121$, $t = -0.750$, $p = 0.457$) and the interaction with the context ($B = 0.470$, $t = 1.514$, $p = 0.137$).

Regarding cooperation, we found that the sum of SMM in the group was not related to contributions in the PGG, either as a main effect ($B = 1.865$, $t = 0.270$, $p = 0.787$) or in interaction with the context ($B = -14.448$, $t = -1.041$, $p = 0.299$). Similar results were found using the maximum individual SMM of the group as a measure of group formidability regarding main effects ($B = -19.077$, $t = -0.864$, $p = 0.388$) and the interaction with the context ($B = -69.333$, $t = -1.564$, $p = 0.119$).

Discussion

In this paper, we tested several predictions derived from the male warrior hypothesis^{8,14}. First, we replicated previous results^{4,15,19,71} about the importance of the intergroup conflict scenario in promoting cooperation within group members and aggression toward outgroup members. We then tested specific predictions about the hormonal underpinnings of male cooperation and aggression during intergroup conflict, concretely the role of an indirect measure of developmental T levels in both behaviors and in a context of intergroup conflict versus a control context without an outgroup threat. In this case, we found only partial support for our predictions since only muscle mass, an indirect marker of pubertal T levels, seems to be associated with aggression and cooperation in the predicted direction when the context is taken into account. Finally, we did not find evidence that the formidability of the group affected individual rates of aggression or cooperation, controlling for individual characteristics.

The male warrior hypothesis is founded on the importance of intergroup conflict for the reproductive success of individuals, especially men. This framework argues that men have physical and psychological traits selected in the context of intergroup competition. Several investigations have shown that men, in fact, tend to show ingroup favoritism and outgroup hostility, a phenomenon known as “parochial altruism”^{72–74}. In this study, we replicated this finding showing that on average individuals were more cooperative in a public good game, that is, they contribute more to the common pool when they competed against another group in order to first reach a threshold, than when they played the game in order to reach the same threshold but without the threat of an outgroup. Further, although most individuals contributed 3,000 Chilean pesos or more, which was the minimum amount to reach the threshold considering an equal contribution, we found that among individuals that contributed 3,000 pesos or more, those in the experimental context behaved more altruistically, that is, they contributed more than those in the control condition. The contributions of individuals that did not invest at least 3,000 pesos were not

different between the two conditions. In other words, individuals in the experimental context decided to invest far more than the minimum to reach the threshold under an equal contribution. If one assumes that there is an implicit norm under this scenario, namely to contribute 3,000 pesos, the difference between both treatments is driven by the supererogatory behavior of some agents whose extra contribution could be understood as a status-seeking strategy. Moreover, individuals behaved more aggressively during the PSAP when they were collectively competing against another group (experimental condition) than when they were competing individually against an individual from an outgroup. Then, aggression was heightened by intergroup conflict even if this aggression was in some sense spiteful, as it was costly for the aggressor and the receiver. In fact, rates of aggression correlated negatively with profits in our study, and the average benefits of individuals in the intergroup conflict context were lower as a consequence. Our results support previous findings about the importance of intergroup competition in cooperation with members of the group and aggression against the members of a competing group.

We were also interested in the hormonal underpinnings of this phenomenon. Testosterone is an androgenic hormone that, among other functions, has been proposed to be a key factor in calibrating cooperative and aggressive responses in different contexts⁹. More concretely, the indirect measures of developmental T levels are expected to be associated with aggressive responses in general and intergroup conflict scenarios^{37,38,41,42}. In this study, we tested the indirect effect of developmental T levels with rates of aggression in a context of intergroup conflict and in a control context. First, we found some support for the claim that an indirect measure of developmental T levels is important in determining levels of aggression. Concretely, we found that body muscularity is a positive predictor of rates of aggression in the intergroup conflict scenario, as well as in the control scenario. However, we did not find any effect of the fWHR or 2D:4D. The fWHR has been related to aggression, both self-reported and as measured by the PSAP³⁰, although the relationship between the fWHR and aggression may be moderated by social status⁷⁵. However, a recent study that evaluated the fWHR and bicep circumference found that bicep circumference was a significant predictor of aggression in the PSAP, while the fWHR was not⁷⁶. Our results are in accordance with those of the latter study in suggesting that body muscularity is the key factor related to aggression and that the fWHR is a correlate of potential physical threat⁷⁶. Evidence of the relationship between 2D:4D and aggression comes mainly from self-reports of aggressive behavior rather than behavioral measurements obtained in a laboratory paradigm, and their effects are small³⁷. In our study, 2D:4D was not a significant predictor of aggressive response in the PSAP in either condition. 2D:4D is probably a reliable indicator of psychological predisposition to aggression, but the real physical power of individuals limits this predisposition under realistic conditions. Using a war game, McIntyre *et al.*³⁸ found more strategic than direct use of aggression. Another explanation of this null result can be found in the proposal of Manning *et al.*²⁹ of an indirect effect of 2D:4D on competitive/aggressive behavior, in which 2D:4D predicts spikes in circulating T, which is a promotor of aggressive behavior through increases in T. Future studies should include measuring circulating T and other forms of aggression to discard or demonstrate a role of 2D:4D in aggressive behavior in the scenario of intergroup conflict.

Regarding cooperative behavior, we found that muscle mass was an important variable in determining individual levels of contribution in the Public Good Game. The effect was moderated by context, that is, more muscular men behaved more cooperatively in the intergroup conflict condition and less cooperatively in the control condition. This supports the prediction that the indirect measure of developmental T levels enhances ingroup cooperation when facing an outgroup threat. These results are similar to those of Stirrat & Perret¹⁹, who showed that the fWHR is related to contributing more or less in a Public Good Game, depending on the context (between groups versus within groups). However, we tested both fWHR and muscle mass and only found a significant effect of muscle mass in cooperation. This result adds further evidence about the importance of the intergroup context in moderating the relationship between the indirect measure of pubertal T levels and cooperation in men and suggests that muscle mass plays a more prominent role in cooperation during intergroup conflict. Less muscular men behaved more cooperatively under our control condition. A possible explanation is that our indirect measure of pubertal T levels, muscle mass, enhances anti-social behavior when there is no outgroup threat. The latter probably occurs because physical power is a reliable cue for fighting ability^{18,77,78} that serve to subdue ingroup rivals and acquire social status and benefits through the use of non-cooperative displays (for instance, the use of anger in⁵³. Given that most individuals contributed at least 3,000 pesos in the Public Good Game, that is, most individuals cooperated in the game, we suggest the control condition can be understood as a scenario based on the balance of cost-benefits of obtaining social status through prestige. In the context without outgroup threat, individuals with traits denoting lower indirect measure of pubertal T levels have the opportunity to gain status through prestige in a context in which competitive traits are less important²⁴. However, when cooperation is triggered by intergroup competition, individuals with traits denoting indirect measure of pubertal T can be expected to cooperate more^{14,19}. We speculate that this is a reliable way to maintain previously acquired ingroup status, and to maintain group structure. According to prenatal T, we did not find any relationship between 2D:4D and cooperation. Although previous studies have reported inconsistent results about the relationship between 2D:4D and cooperation^{44–46,79,80}, it is plausible that indirect measure of prenatal T has a more indirect role in the expression of cooperation in the intergroup conflict scenario, as with aggression. In a study with female subjects⁸¹, inoculating testosterone only increased cooperation among participants with a lower 2D:4D ratio.

We did not find evidence that individuals adjust their behavior according to the formidability of the group. This is a key prediction of the male warrior hypothesis⁸, which, to our knowledge had not been tested until now. There are several possible explanations for the absence of any indication of the influence of group composition. Our expectation that individuals would adjust their behavior in the same way according to the composition of the group may have been too simplistic. It is possible that the effect of group formidability only manifests itself with a few individuals who act as leaders, while weaker individuals rely on the strength of the leaders. Another explanation is that because members of one group are not able to assess the formidability of the outgroup, they calibrate

their behavior based on their day-to-day experience about the formidability of the group, which may vary among individuals in the same group and among groups. In any case, previous studies suggest that individuals can assess the formidability of other groups. Therefore, future studies should focus on determining if this ability translates into calibrating individual behavior according to group composition compared with the outgroup.

Our study has several limitations that have to be considered in appraising the scope of our results. First, we have not measured the degree of friendship among the participants. However, our statistical design allowed us to control for variability in aggression and cooperation between groups. In any case, we are beginning to test this variable for a new project, and although it is clear that an interaction scenario affects the behavior of participants, it would be interesting to test the possible effect of the previous history of the relationship on strategic behavior in the context of both aggression and cooperation. In addition, we have not considered the inclusion of psychological variables that could moderate the expression of the tested behavior, such as self-perceived social status, general aggression, and social value orientation. Finally, although we have demonstrated that outgroup aggression and ingroup cooperation are exacerbated among men engaged in intergroup contests, we cannot deny the possibility this effect is also present among women. In the future, we expect to study this issue among women.

To conclude, our results from applying an experimental design under controlled conditions support one of the main predictions of the male warrior hypothesis, that aggression and cooperation are heightened in groups of men in the context of intergroup conflict. Our analysis of the effects of developmental testosterone on aggression and cooperation further supports the notion that body muscularity is an important trait that influences the intensity of aggressive responses under provocation, as measured in the PSAP. Notably, the relationship between body muscularity and aggression is not dependent on the context (intergroup conflict versus control). In our study, the context of intergroup aggression increased the rates of aggression independent of testosterone. In other words, men seem to increase aggression regardless of their body muscularity. Our results indicate that context influences and increases cooperative behavior in men. Muscularity affects cooperativeness, more muscular men being more cooperative than less muscular counterparts in the intergroup scenario, but with the reverse effect in the control situation (only with the intragroup scenario).

Future studies are needed that include circulating T and analysis of this effect in interaction with anthropometric indicators of developmental T levels. More complex experimental designs are needed to include the assessment of the rival group's formidability. The mechanisms (if they exist) are more likely to be noted if a visual comparison is made before the competition.

Data availability

The data set generated and employed in this study is available from the corresponding author upon request.

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Author contributions

J.A.M.R. and P.Po. conceived the study. J.A.M.R., P.Po., N.V., P.Pa., D.D. and M.P. designed the experiments and protocols. J.A.M.R., P.Po., N.V., P.Pa., O.R.H. and O.F. collected the data. P.Po. and J.A.M.R. analyzed the data. J.A.M.R., P.Po. and C.R.S. drafted the manuscript. All the authors reviewed and edited the manuscript.

Competing interests

The authors declare no competing interests.

Additional information

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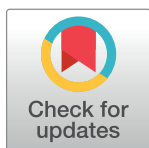
RESEARCH ARTICLE

Testing strategic pluralism: The roles of attractiveness and competitive abilities to understand conditionality in men's short-term reproductive strategies

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Abstract

The decision to allocate time and energy to find multiple sexual partners or raise children is a fundamental reproductive trade-off. The Strategic Pluralism Hypothesis argues that human reproductive strategies are facultatively calibrated towards either investing in mating or parenting (or a mixture), according to the expression of features dependent on the individual's condition. This study seeks to test predictions derived from this hypothesis in a sample of 242 young men ($M \pm SD = 22.12 \pm 3.08$) from Chile's 5th Region (33° south latitude). Specifically, two predictions were considered that raise questions about the relationship between traits related to physical and psychological attractiveness (fluctuating facial asymmetry and self-perception of attractiveness) and competitive skills (baseline testosterone and self-perception of fighting ability) with short-term reproductive strategies. Our results indicate that psychological features related to the self-perception of physical attractiveness are related to short-term reproductive strategies. However, no evidence was found that fluctuating facial asymmetry, basal levels of testosterone and self-perception of fighting ability were related to short-term reproductive strategies. These results support the existing evidence of the importance of physical attractiveness in calibrating men's reproductive strategies but cast doubts about the role of fluctuating facial asymmetry. They also suggest that traits related to physical attractiveness, in comparison to competitive capabilities, play a more important role in calibrating men's short-term reproductive strategies.

Data Availability Statement: All relevant data are within the manuscript and its Supporting Information files.

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Introduction

Reproductive strategies can be defined as an integrated set of adaptations that constitute solutions to different reproductive compromises or trade-offs that the individual faces [1]. The Strategic Pluralism Hypothesis seeks to explain inter- and intra-individual variation in human reproductive strategies based on the expression of traits dependent on the condition of the individual in interaction with the environment. This hypothesis emphasizes the costs and benefits for men and women concerning the resources invested in seeking partners versus providing parental care [1, 2]. In mammals, the trade-off for males between the search for a partner and parental care is particularly relevant given that males invest less than females in obligatory parental care while having a higher potential reproductive rate [3]. This means that for males, including men, maximizing reproductive success is mainly constrained by the degree of access to multiple reproductive partners [3, 4]. However, biparental care in humans may represent an important factor that affects offspring survival and, then, constrains men's reproductive success as well [5]. According to the Strategic Pluralism Hypothesis, individuals would display a mixture of short and long-term reproductive strategies, reflecting different degrees of investment in mating versus parenting effort according to individual phenotypic features and ecological and social conditions [1]. In this sense, the ability to attract partners and to compete with individuals of the same sex are two factors that affect the degree of investment in short-term reproductive strategies, given that they reduce the costs-benefits balance of investing in mating [6]. Consequently, the integrated study of these two factors is key to understanding their influence on short-term reproductive strategies.

Physical attractiveness is directly related to the capacity of being chosen as a mate [6–8]. Research in this field has identified a series of bodily features associated with attractiveness, facial symmetry being one of these [9, 10]. Fluctuating facial asymmetry has been proposed as an indicator of individual quality that reflects the capacity of an individual to maintain a symmetric pattern of stable development [9, 11]. However, there is mixed evidence supporting the notion of fluctuating asymmetry as a reliable indicator of the degree of developmental stability and individual quality [12–14]. In turn, fluctuating facial asymmetry is assumed to underlie individual differences in facial symmetry and, consequently, in attractiveness, but this assumption is rarely tested. Despite this, some studies suggest that men with relatively lower levels of fluctuating facial asymmetry are more attractive to women, especially for short-term relationships, are more economically successful, less faithful, and less inclined to invest in their progeny [15–18]. These results are consistent with evidence that men with lower levels of fluctuating facial asymmetry have more sexual partners and tend to be more direct in approaching the opposite sex in courtship, a characteristic that is related to short-term or unrestricted reproductive strategies [1, 8, 14, 19, 20]. Nevertheless, other investigations [10, 21] have not been able to replicate the association between the number of sexual partners and fluctuating facial asymmetry in men. These contradictory findings indicate the need to generate new studies in the field including psychological variables that may influence the relationship between fluctuating facial asymmetry and reproductive success to further test the relevance of fluctuating facial asymmetry as a signal of quality. Particularly relevant for our study is the relationship that has been observed between self-perception of physical attractiveness and the prevalence of short-term reproductive strategies since there is an association between self-perceived characteristics and received social signals, which together affect behavior. That is, the assessment of one's attractiveness is associated with short-term strategy because it reflects the preference of women for certain traits [6, 22, 23].

At the level of competitive abilities, intrasexual competition is another component that influences access to partners of the opposite sex [6, 24]. Testosterone is related to the

development of the traits and behaviors related to intrasexual competition, as the display of direct physical aggression [25]. Testosterone is an androgenizing hormone with two main types of effects: organizational and activational. At the organizational level, it has an androgenizing effect during the prenatal stage and at puberty. At the activational level, baseline testosterone levels, as well as changes in circulating testosterone levels, have been associated with behavioral changes related to intrasexual competition and reproductive effort [26–28]. Focusing on baseline testosterone, there is evidence that baseline testosterone levels are positively related to dominance, competitiveness [28, 29], and especially aggression [30], although this effect depends on the specific context [27], and some studies reported a lack of evidence for the mentioned relationships [31]. Lower baseline testosterone levels have been associated with men's relational status and paternity; that is, baseline testosterone levels are lower in men involved in long-term relationships, and especially in those that are fathers [32, 33, for a review see 34]. However, these levels can be expected to remain high in men who, although involved in a relationship, are interested in having extramarital relationships [35–37]. Puts et al. [38] studied the relationship between testosterone levels and three dimensions of sociosexuality: sociosexual desire, sociosexual behavior, and sociosexual attitudes. Their results indicate that testosterone levels are positively related to unrestricted sociosexual psychology (desires and attitudes), which results in a larger number of reproductive partners (behavior). However, they found that the number of reproductive partners has a negative effect on testosterone levels. They interpret these findings as a negative feedback mechanism that prevents maintaining high testosterone levels once sociosexual desires have been satisfied [38]. This suggests that testosterone plays an important role in the willingness of individuals to compete for reproductive partners, which in turn implies searching for short-term strategies. This relationship is complex because there are negative regulatory mechanisms. At the psychological level, testosterone increases competitive behavior and reduces cooperation in determined contexts [29] suggesting that testosterone levels influence intrasexual competition and reproductive success [28, 36, 39]. In addition, the self-perception of having traits related to resource holding potential, like being a good fighter, may be positively related to signs of dominance in competitive contexts [40] suggesting that this psychological feature plays a role when competing for mating.

Competitive abilities and physical attractiveness do not act independently. Lukaszewski et al. [23] examined the effect of body strength as an indicator of both fighting ability and attractiveness, and the self-perception of physical attractiveness, as well as the assessment by third parties of physical attractiveness and sociosexual attitudes and behaviors. Their results show that self-perception of physical attractiveness mediates the positive effect between physical strength, unrestricted socio-sexual attitudes, and the number of sexual partners. This indicates the need to explore how indicators of physical attractiveness and fighting ability explain unrestricted human reproductive strategies, using a larger number of morphological, physiological and psychological indicators.

Considering all of the above, we can establish that attractiveness and competitive abilities are important elements that according to the Strategic Pluralistic Hypothesis are expected to play a major role calibrating unrestricted reproductive strategies, especially when a combined effect of the two is displayed. However, there have been few studies that consider biological (morphological and physiological) and psychological variables in an integrated manner in order to understand how reproductive trade-offs are dealt with. The objective of this study is to investigate how the features of physical attractiveness and competitive abilities influence short-term male reproductive strategies and how psychological features may act as moderators of these effects. To do this, fluctuating facial asymmetry and the self-perception of physical attractiveness are considered as anthropometric and psychological features of physical attractiveness. Likewise, the levels of circulating baseline testosterone and self-perception of fighting

ability are considered physiological and psychological features associated with competitive capacity. Considering the postulates of the Strategic Pluralism Hypothesis, we should expect a positive association between features signaling physical attractiveness and competitive capacity with short-term reproductive strategies because both sets of traits decrease the costs associated with seeking and competing for mates and satisfy the short-term mating preferences of women. Our particular predictions are as follows: (1) fluctuating asymmetry should be negatively associated with short-term reproductive strategies, especially in individuals with high levels of self-perceived physical attractiveness, whereas basal levels of testosterone should be positively associated with short-term strategies, especially in those individuals with high levels of self-perceived fighting ability; (2) the individual's competitive abilities are expected to moderate the effect of attractiveness on short-term reproductive strategies. In this way, attractiveness has a positive effect on short-term reproductive strategies that is greater for individuals who display higher competitive abilities.

Materials and methods

Ethics statement

The research was approved by the ethics committee of Universidad de Playa Ancha. Participants signed a written informed consent before they participated in the study.

Participants

The initial sample was composed of 246 young men. However, three individuals were rejected because they failed to complete some of the questionnaires and one individual failed to provide a photo, so the sample was reduced to 242 men between 18 and 35 years of age ($M \pm SD = 22.12 \pm 3.08$). The participants were recruited using ads posted in universities in the 5th Region of Chile (33° south latitude). In terms of sexual orientation, 97.5% stated they were heterosexual and 3.5% stated they were homosexual. In terms of relational status, 53.8% stated they were in a couple at the time of participating in the investigation.

The participants received an economic reimbursement of five thousand Chilean pesos (approximately seven US dollars) as an economic reimbursement for participating, plus up to 30,000 pesos (approximately 43 USD and almost twice of the daily minimum wage) conditional on their performance in the economic games that were played as a part of a wider experimental procedure. These games were introduced and played after the measurement of basal testosterone and after the participants answered the questionnaires. Consequently, these games were not expected to affect responses and measures considered in this study.

Psychological measurements

Sociosexual Orientation Scale (SOI). We used a multidimensional version of the SOI developed by Jackson & Kirkpatrick [41] that had been applied previously with Chilean subjects [see 42]. The scale is divided into attitudinal and behavioral dimensions. There are two attitudinal factors that measure sociosexual orientation in the short-term (e.g. "I can easily imagine being comfortable with and enjoying casual sex with different women", 10 items) and long-term (e.g. "I am interested in maintaining a long-term romantic relationship with a special woman", 7 items). These factors are in the format of 7-point Likert scale responses in which 1 indicates "strongly disagree" and 7 indicates "strongly agree". The behavioral dimension consisted of 5 items of open-ended responses that included questions about the number of sexual partners in the past (3 items) (e.g. "Over your entire life, how many women have you had complete sexual relations with?"), a question about sexual fantasies (How often do you

fantasize about having sexual relations with women other than your current partner?) and a question about the expected number of sexual partners in the future (How many women do you think you will have sexual relations within the next five years). This study only considered the items referring to the attitudinal factor in short-term relationships. Polo et al. [42] obtained a Cronbach α value of .95 for the aforementioned factor, while a Cronbach α of .70 was obtained in the present study, indicating that the instrument is sufficiently reliable.

Self-perceived fighting ability questionnaire. We used a version of the self-perceived fighting ability questionnaire developed by Muñoz-Reyes et al. [25], which had been applied previously with Chilean subjects [see 43]. This is a short 4-question questionnaire that assesses the self-perception of fighting skills (1. How good a fighter am I? 2. How do others perceive my abilities as a fighter? 3. How much fear can I provoke in someone who is about to fight me? 4. What are my odds of winning a fight if I have to fight someone?). The responses are on a seven-point Likert scale in which 1 indicates "well below average" and 7 indicates "well above average". Muñoz-Reyes et al. [43] obtained a Cronbach α score of .84 in the original study. In the present study, an α coefficient of .87 was obtained, indicating adequate reliability for the studied sample.

Self-perception of attractiveness. This consists of a single question to assess self-perception of physical attractiveness (How attractive do you think you are?). The response is on a 7-point Likert scale in which 1 indicates "not attractive at all" and 7 indicates "very attractive".

Anthropometric and physiological measurements

Fluctuating facial asymmetry. This indicator of attractiveness is measured according to the protocol of Sanchez-Pages & Turiégano [44]. Frontal photographs were taken of the participants with a Nikon D-90 camera under constant conditions of light, head orientation, focal length (3 m), shutter speed (1/60 s) and aperture ($f/5.6$). Participants were asked not to wear any form of facial adornment and to maintain as neutral an expression as possible. Photos where the subject smiled or inclined his head were rejected and we selected the best photo of each participant. Fluctuating facial asymmetry was calculated based on 106 facial points or landmarks (LM), which were obtained with the program FACE ++ [see 45 for a similar procedure, 46] from the selected photos. This software identifies high-precision facial reference points, like facial contours, eyes, eyebrows, and nose. The use of this software was automated with a MatLab software algorithm connected to the interface of programming applications of FACE ++. Fluctuating facial asymmetry was determined with the software MorphoJ [47] (also see http://www.flywings.org.uk/MorphoJ_page.htm) based on the Procrustes distances between each LM the corresponding mirror image LM. These distances reflect both directional and fluctuating asymmetry but can be decomposed in these two components employing a Procrustes ANOVA analysis since Procrustes coordinates are based on the algebra of sums of squares [48, 49]. In this sense, the variance attributable to the variable "side of the face" corresponds to directional asymmetry, whereas the variance attributable to the interaction between "side of the face" and "individual" corresponds to fluctuating asymmetry. In other words, fluctuating asymmetry was calculated as the deviation of each individual's asymmetry from the overall average asymmetry in units of Procrustes distance. Accordingly, higher values represent higher levels of individual fluctuating asymmetry than lower values. In addition, we calculated the distribution of the differences between each LM and the corresponding mirror LM from each individual and each coordinate in order to characterize the nature of the variation in the asymmetry component. We found that differences between LM in the horizontal axis were normally distributed in 44 out of 48 pairs of LM, whereas differences between LM in the vertical axis were normally distributed in 45 out of 48 pairs of LM.

Baseline testosterone. Baseline testosterone was measured with a 1-ml sample of saliva of the participants, who were asked not to eat or drink anything other than water for at least one hour before the sample was taken. The samples were taken at approximately noon to avoid alterations in testosterone levels as the result of circadian hormonal variation. A passive saliva collection method (Salimetrics®) was used to collect samples. After being collected, the samples were centrifuged, frozen and stored at -20°C in cyrotubes (SalivaBio®) for 20 days. All the samples were analyzed with the Testosterone Enzyme Immunoassay Kit (Salimetrics®) in accordance with manufacturer's instructions. Due to a problem with storing the saliva samples (freezing rupture and consequent increase in temperature), 136 individuals were not included in the baseline testosterone analysis because the intra and interplate variation coefficients were very high. Thus, the sample for all the baseline testosterone analyses was 106 individuals between 18 and 35 years of age ($M \pm SD = 22.34 \pm 3.08$). The coefficients of intraplate and interplate variation were respectively equal to and less than 15%.

Statistical analysis

To test our predictions, we fitted one general linear model in three successive steps. The two first steps tested our first prediction and the third step tested our second prediction. Fluctuating facial asymmetry, basal levels of testosterone, self-perception of physical attractiveness and self-perception of fighting ability were considered independent variables, and short-term socio-sexual orientation was considered the dependent variable. The age and relational status of the subjects were also considered as control variables. Independent and control variables were centered on their means. In a first step, we fitted only the main effects in the model. In the second step, we added the interaction terms between fluctuating asymmetry and self-perception of physical attractiveness and between basal levels of testosterone and self-perception of fighting ability. In this way, we tested our first hypothesis taking into account that nonsignificant interactions may preclude to assess main effects. Finally, we added the interaction term between fluctuating asymmetry and basal levels of testosterone and between self-perception of physical attractiveness and self-perception of fighting ability to test our second prediction. Because of the reduced sample size with the introduction of the baseline testosterone variable and because it did not have a statistically significant effect on the model, the variable was eliminated to restore the complete sample. A similar analytical strategy was used to test our predictions but without basal testosterone levels and using the full data set. Consequently, we finally fitted two models, one with the reduced data set and the other one with all the data available, in three successive steps.

The normality of residuals was verified for the two models and IBM SPSS 21.0 software was used for the general linear models. The level of significance was set at $\alpha = .05$.

Results

Table 1 shows the descriptive statistics for the morphological, physiological and psychological variables. First, we show the results considering the reduced data set, that is, the model that considers baseline testosterone levels. We did not find any significant main effect of our variables (see Table 2). When introducing the predicted interactions between physical and psychological variables, we found that self-perception of physical attractiveness did not moderate the predicted relationship between fluctuating facial asymmetry and unrestricted sociosexual orientation ($B = -236.910$, $t = -.685$, $p = .495$). Similarly, the self-perception of fighting ability did not moderate the predicted relationship between basal testosterone levels and unrestricted sociosexual orientation ($B = .002$, $t = .473$, $p = .638$). Finally, when we considered the interaction between attractiveness and competitive traits at both levels (physical and psychological),

Table 1. Descriptive statistics for the variables employed in this study.

Variable	Reduced sample (N = 106)		Full sample (N = 242)	
	M ± SD	Range (min, max)	M ± SD	Range (min, max)
Age	22.34 ± 3.08	18, 35	22.12 ± .3.08	18, 35
FFA	.016 ± .005	.008, .033	.016 ± .005	.008, .033
Basal testosterone	212.18 ± 75.91	94.31, 506.80		
SPPA	4.77 ± .99	2, 7	4.68 ± .97	1, 7
SPFAQ	17.26 ± 4.78	5, 28	16.80 ± 4.88	4, 28
Short-term SOI	44.63 ± 13.62	10, 70	44.45 ± 13.42	10, 70

Fluctuating facial asymmetry (FFA), self-perception of physical attractiveness (SPPA), self-perception of fighting ability (SPFA), short-term sociosexual orientation inventory (Short-term SOI).

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we did not find that the interaction terms were significant, that is, basal testosterone levels did not moderate the predicted relationship between fluctuating facial asymmetry and unrestricted sociosexual orientation ($B = 1.783, t = .435, p = .665$), and self-perception of fighting ability did not moderate the predicted relationship between self-perception of physical attractiveness and unrestricted sociosexual orientation ($B = .296, t = 1.125, p = .263$). Overall, our results with the reduced data set showed that no variable was related to unrestricted sociosexual orientation neither when considering main effects nor the predicted interactions.

When considering the full data set, that is, setting aside the basal levels of testosterone, we found a positive relationship between the self-perception of physical attractiveness and unrestricted sociosexual orientation when fitting main effects ($B = 2.074, t = 2.215, p = .028$; see [Table 3](#) and [Fig 1](#)). However, neither fluctuating facial asymmetry ($B = 208.547, t = 1.104, p = .271$) nor self-perception of fighting ability ($B = .195, t = 1.053, p = .293$) were related to unrestricted sociosexual orientation. Moreover, self-perception of physical attractiveness did not moderate the predicted relationship between fluctuating facial asymmetry and unrestricted sociosexual orientation ($B = -203.254, t = -.945, p = .346$). And finally, self-perception of fighting ability did not moderate the predicted relationship between self-perception of physical attractiveness and unrestricted sociosexual orientation ($B = .309, t = 1.742, p = .083$). Overall, our results with the full data showed a positive effect of self-perception of physical attractiveness over unrestricted sociosexual orientation being the other predicted effects non-significant.

Table 2. General linear model for short-term sociosexual orientation considering the reduced data set (N = 106).

Model	R^2_{adj}	p		B	t	p	η^2_p
Main effects	.041	.116	Intercept	47.568	22.937	< .001	.842
			RS = Paired	-5.107	-1.814	.073	.032
			Age	.306	.708	.481	.005
			Basal testosterone	.011	.611	.543	.004
			FFA	190.731	.691	.491	.005
			SPPA	1.594	1.106	.271	.012
			SPFA	.535	1.759	.271	.012
Interaction terms (1)	.028	.213	FFA * SPPA	-236.910	-.685	.495	.005
			Basal testosterone * SPFA	.002	.472	.638	.002
Interaction terms (2)	.037	.167	FFA*Basal testosterone	1.783	.435	.665	.002
			SPPA*SPFA	.296	1.125	.263	.013

Relational status (RS), fluctuating facial asymmetry (FFA), self-perception of physical attractiveness (SPPA), self-perception of fighting ability (SPFA).

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Table 3. General linear model for short-term sociosexual orientation considering the full data set (N = 242).

Model	R^2_{adj}	p		B	t	p	η^2_p
Main effects	.050	.004	Intercept	46.532	37.430	< .001	.856
			RS = Paired	-3.870	-2.271	.024	.021
			Age	.493	1.772	.078	.013
			FFA	208.547	1.104	.271	.005
			SPPA	2.074	2.215	.028	.020
			SPFA	.195	1.053	.293	.005
Interaction terms (1)	.049	.006	FFA* SPPA	-203.254	-.945	.346	.004
Interaction terms (2)	.058	< .001	SPPA*SPFA	.309	1.742	.083	.013

Relational status (RS), fluctuating facial asymmetry (FFA), self-perception of physical attractiveness (SPPA), self-perception of fighting ability (SPFA).

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Discussion

The Strategic Pluralism Hypothesis explains the conditionality of human reproductive strategies and the resolution of the trade-off between investment in multiple partners and investment in parental care [1]. This hypothesis considers that there are biological, psychological and anthropometric factors that calibrate reproductive behavior according to the context in which the individual faces the aforementioned trade-off. This study proposes two predictions that were mainly not sustained as only an effect of self-perceived physical attractiveness on short-term sociosexual orientation was found. Our results emphasize the role of physical attractiveness in men on the unfolding of unrestricted reproductive strategies (short-term strategies at the scale of sociosexual orientation). The main result indicates that the traits of attractiveness have an effect on unrestricted reproductive strategies whereas fighting abilities do not.

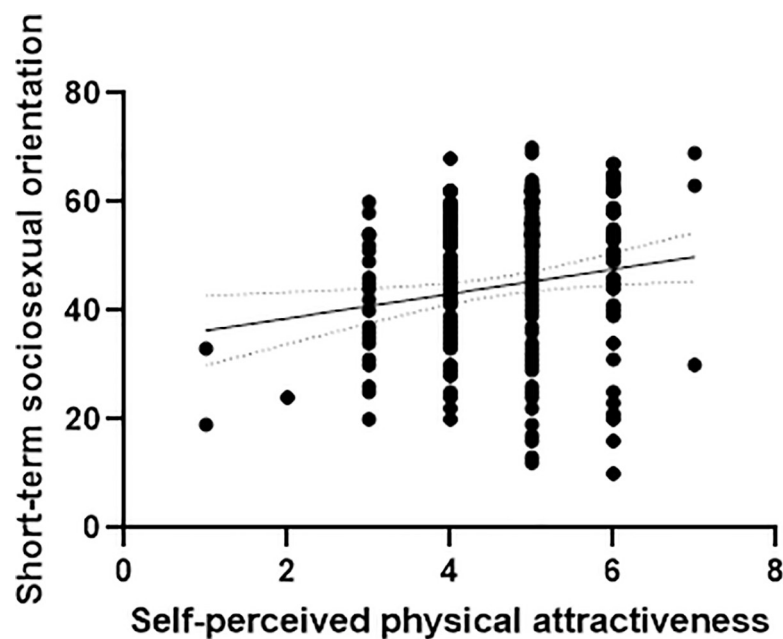


Fig 1. Relationship between self-perceived physical attractiveness and short-term sociosexual orientation. Dots represent observed values. Full line represents expected values across the observed range of short-term sociosexual orientation. Dotted lines represent 95% interval confidence bands of the predicted values.

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The first prediction sought to determine if there is a positive relationship between traits associated with physical attractiveness and traits associated with competitive abilities with unrestricted reproductive strategies. Also, we postulated that these effects should be moderated by psychological variables related to self-perception of physical attractiveness and fighting ability, respectively. Our results suggest that only self-perceived attractiveness does affect unrestricted sociosexual orientation when evaluated with the full data set. However, we failed to show the expected effect of fluctuating facial asymmetry on unrestricted reproductive strategy either as a main effect or moderated by self-perception of physical attractiveness. Conversely to our results, some studies found evidence that fluctuating facial asymmetry is associated with the implementation of short-term reproductive strategies [20], with the number of sexual partners over one's lifetime [50, 51], and with the perception of attractiveness [14]. Several lines of evidence may explain our contrasting results. First, despite that symmetry is associated with attractiveness, this association is weak and other facial features like averageness may play a more important role in perceived attractiveness [52]. Also, facial fluctuating asymmetry is assumed to underlie variation in facial symmetry between individuals being an indirect measure of overall symmetry. This circumstance may lessen its relationships with attractiveness. And more importantly, there exists controversy about the relationship between evolutionary relevant features and levels of fluctuating facial asymmetry [21]. If it is the case that fluctuating asymmetry is not an accurate proxy of developmental instability, the rationale about the importance of fluctuating facial asymmetry as a trait related to short-term mating strategies weakens and other variables as muscularity or strength could be better predictors of an unrestricted sociosexual orientation than fluctuating facial asymmetry [42, 53]. However, this is an unresolved issue as positive evidence about the importance of fluctuating asymmetry as a proxy of health and mating success was also reported [14]. An alternative explanation of our results is that fluctuating facial asymmetry affects unrestricted sociosexual orientation but this effect is mediated rather than moderated by psychological features. In this regard, previous investigations have found that the effects of morphological features on the psychology of unrestricted male sociosexual behavior were mediated by self and third-party perceptions of physical attractiveness [23, 54]. However, our cross-sectional design precluded us to investigate mediation relationships in an accurate way [55].

Self-perception of fighting ability was not related to unrestricted sociosexual orientation. In this regard, other studies have established a relationship between fighting and mate value [43], which is defined as “the complete set of characteristics that an individual has in a given moment and in a particular context that affects his capacity to successfully find, attract and keep a partner” [56]. According to Muñoz-Reyes et al. [43], fighting ability is associated with the mate value of a partner, which implies a positive relationship between this variable and men's assessments of their chances of finding partners, and therefore of employing intrasexual competition strategies, which implies a high degree of self-confidence in the search for partners. It has been established that the self-perception of fighting ability is also associated with aggressive behavior [25]. These findings indicate that it is plausible to support that fighting ability is a conflict resolution mechanism in situations of intrasexual competition, which is consistent with studies that have found a positive association between traits associated with fighting abilities and reproductive success [23, 43, 57]. Despite the above evidence, our null results may indicate that self-perception of fighting ability when evaluated jointly with self-perception of attractiveness is not an important factor related to unrestricted strategies. That can be explained if we assume that mate choice or indirect competition through showing off attractive features may be more important in industrialized societies rather than the direct competition through fights.

No effect was found for baseline testosterone levels on short-term reproductive strategies. Studies have associated testosterone with the search for social status [58], self-confidence in

competitive situation [39] and the adoption of dominant roles in economic environments [29]. Consequently, testosterone can be considered a social hormone associated with status-seeking and not so much with aggression in itself. Status in turn could be related to different reproductive strategies according to the way it is acquired. The relationship between testosterone and reproductive strategies has been explored in other studies and evidence has been found that favors the role of testosterone as a promoter of short-term strategies. For example, Edelman et al. [32] found an interaction between unrestricted sociosexuality and the relational status of men and established that men in relationships with partners, but that have interest in extramarital relationships, have similar testosterone levels as those of single men, producing a positive attitude about unrestricted strategies. Puts et al. [38] established that there is a negative relationship between the number of sexual partners and baseline testosterone levels, and a positive relationship between high levels of baseline testosterone and unrestricted sociosexual psychology (desire and attitudes). Although this investigation employed a reduced version of the sociosexual orientation questionnaire [59], a relationship was found between baseline testosterone levels and an orientation toward short-term strategies. The reduced sample in the model that assesses the effect of baseline testosterone on reproductive strategies could explain the null result with respect to this variable.

Based on the second prediction, a relationship was expected between attractiveness and competitive abilities on unrestricted strategies. We failed to find that association as the effect of self-perception of attractiveness was not moderated by self-perception of fighting abilities. This result further suggests that fighting abilities do not play a major role in unrestricted sociosexual orientation both directly or moderating the effects of physical attractiveness. In addition, it is important to consider that self-perception of fighting ability may not necessarily be related to the willingness to compete for new mates, but may be also associated with the willingness to protect a current mate and the offspring. In this regard, that feature is expected to be related to more restricted sociosexual orientation reflecting a higher inversion in parental care [6].

Among the limitations of this research is the inclusion of only one anthropometric measurement (fluctuating facial asymmetry), which, although a common measurement to study physical attractiveness, could be complemented with others that are also considered attractive features and, in some cases, more important in explaining facial attractiveness [52]. Another limitation was the loss of data due to the storage of samples and handling of the testosterone kit, despite following protocols tested in other investigations. In addition, our null results of the effect of basal testosterone on sociosexuality do not preclude a potential relationship between testosterone changes elicited on a mating context and sociosexuality. Changes in testosterone levels and additional anthropometric variables associated with unrestricted strategies should be included in future research, such as facial masculinization [35], height [e.g. 60] and body mass [e.g. 42]. Finally, individuals in our study expected to participate in a competitive game and to be paid according to their performance. Despite that these tasks were performed after the measures taken for the current study; they may introduce some noise in the study.

In conclusion, the present study contributes some evidence that supports the Strategic Pluralism Hypothesis as we found that psychological features of attractiveness are related to unrestricted reproductive strategies among men. However, our results are not conclusive about the potential role of competitive skills (measured by basal levels of testosterone and self-perception of fighting ability) and the role of fluctuating facial asymmetry in explaining unrestricted reproductive strategies. These findings encourage further research on traits that may be affecting the cost-benefits balance in the reproductive trade-off that men have between maximizing the number of sexual partners and investing in parental care, and designs that allowed to investigate mediation relationships considering the importance of the relationship among

anthropometric features on the self-perception (that is, psychological features) of subjects when the reproductive trade-off is solved.

Supporting information

S1 Dataset.

(XLSX)

S1 File. Normality and t tests.

(PDF)

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