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Who is the fairest of them all? The independent effect of attractive features and self-perceived attractiveness on cooperation among women

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### 27 ABSTRACT

28 The present paper analyzes the extent to which attractiveness-related variables affect cooperative behavior in women. Cooperativeness is evaluated through a Prisoner's 29 Dilemma Game (PDG). We consider several morphometric variables related to 30 attractiveness: Fluctuating Asymmetry (FA), Waist-Hip Ratio (WHR), Body Mass Index 31 (BMI) and *Facial Femininity* (FF). These variables have been shown to predict human 32 33 behavior. We also include as a control variable a score for Self-Perceived Attractiveness (SPA). We test differences in these variables according to behavior in the PDG. Our 34 results reveal that low FA women cooperate less frequently in the PDG. We also find 35 36 that women with lower WHR are more cooperative. This result contradicts the expected relation between WHR and behavior in the PDG. We show that this effect of WHR on 37 cooperation operates through its influence on the expectation that participants hold on 38 39 the cooperative intent of their counterpart. In addition, we show that the effect of attractive features on cooperation occurs independently of the participants' perception of 40 their own appeal. Finally, we discuss our results in the context of the evolution of 41 cooperative behavior and under the hypothesis that attractiveness is a reliable indicator 42 of phenotypic quality. 43

44

45 Keywords: Cooperation; Attractiveness; Fluctuating asymmetry; Waist-hip ratio; Body
46 Mass Index; Facial Femininity.

### 47 **<u>1.0 INTRODUCTION</u>**

48

Human cooperation is an undeniably appealing phenomenon which has attracted 49 substantial attention from scientists (Hammerstein, 2003). One line of research on 50 cooperative behavior has obtained important insights by using strategic games (e.g. 51 Burnham, 2007; Eisenneger et al. 2010; Kosfeld et al. 2005; Lovejoy et al. 2013; Millet 52 53 & Dewitte, 2006; Mulford et al. 1998; Sanchez-Pages & Turiegano, 2010, 2013; Takahashi et al. 2006; Van den Bergh & Dewitte, 2006; Zaatari & Trivers, 2007; Zak et 54 al. 2009, Zethraeus et al. 2009). In strategic games, participants face simplified social 55 56 situations in the laboratory and receive rewards depending on their decisions as well as those of other participants. Because these studies use controlled environments, the 57 behavior displayed by subjects is easily measurable and replicable. 58

59

In the present study, we define cooperation as an individual behavior aimed to 60 maximize collective interest rather than pure self-interest. One way of evaluating 61 cooperation with strategic games is through the Prisoners' Dilemma (PDG henceforth). 62 The PDG is a strategic game in which collective welfare and self-interest are in stark 63 64 conflict. Standard Game Theory postulates that individuals act following their selfinterest only and should hence not cooperate in the PDG, even though such behavior 65 eventually leads to a loss in collective welfare. Early experimental studies demonstrated 66 that such prediction is only partially fulfilled. Even in one-shot situations, and when 67 playing against complete strangers, humans tend to cooperate in the PDG in sizeable 68 69 rates (see Marwell & Ames, 1981 and Dawes & Thaler, 1988, among many). Undoubtedly, it is of a great interest to explore which individual factors, if any, cause 70 some individuals to be more prone to cooperate than others. 71

72	Several recent papers describe the effect of physiology-related variables on
73	human behavior in economic experiments (Apicella et al. 2008; Burnham, 2007;
74	Eisenneger et al. 2010; Kosfeld et al. 2005; Millet & Dewitte, 2006; Van der Bergh &
75	Dewitte, 2006; Zaatari & Trivers, 2007; Zak et al. 2009; Zethraeus et al. 2009).
76	However, few studies have focused on the relationship between individual features and
77	cooperative behavior in two-person interactions like the PDG (Lovejoy et al. 2013;
78	Mulford et al. 1998; Sanchez-Pages & Turiegano, 2010; Takahashi et al. 2006). Even
79	smaller is the number of these studies focusing exclusively on women. This gap in the
80	literature is rather unsatisfactory given the important physiological differences,
81	especially endocrine, that exist between sexes (for exceptions see Buser, 2012; Pearson
82	& Schiepper, 2013).
83	
84	In the present paper, we investigate the relationship between cooperation among
85	women in the PDG and a number of physiology-related variables with well-established

86 effects on human behavior. These variables are Facial Fluctuating Asymmetry, Facial87 Femininity, Waist-Hip Ratio and Body Mass Index.

88

Fluctuating Asymmetry (FA) is a variable with a physiological basis and linked 89 90 to individual's fitness. It can be defined as a departure from symmetry in traits that are symmetrical at the population level (Van Dongen & Gangestad, 2011). FA is considered to 91 be the result of developmental instability, reflecting the ability of an organism to 92 maintain a stable development of its morphology and to overcome possible external 93 perturbations (Møller & Swadle, 1997; Thornhill & Gangestad, 2006; Van Dongen & 94 95 Gangestad, 2011). Consequently, it has been described as linked to individual fitness in many species (Møller, 1997; Møller & Thornhill, 1998). In humans, there exists a 96

positive average effect of FA on a variety of outcomes, from hormone levels to health 97 98 problems. These effects are robust, especially those related to reproduction (Van Dongen & Gangestad, 2012). FA has also been related to human behavior (Furlow et al. 99 100 1998; Holtzman et al. 2011; Manning & Wood, 1998; Muñoz-Reyes et al. 2012; Pound et al. 2007; Zaatari & Trivers, 2007). In particular, FA has been studied in relation to 101 cooperative behavior in males. Results show that low FA males (more symmetric) 102 cooperate less often in the PDG (Sanchez-Pages & Turiegano, 2010). FA is also a 103 determinant of behavior in the Ultimatum Game (Sanchez-Pages & Turiegano, 2013; 104 Zaatari & Trivers, 2007; Zaatari et al. 2009). In both the PDG and in the Ultimatum 105 106 Game (UG henceforth), symmetrical men (with lower FA) tend to be less prosocial. Personality measurements corroborate this finding (Holtzman et al. 2011). One possible 107 explanation for the lack of pro-sociality of symmetrical males is their higher capability 108 109 to obtain resources by themselves, which reduces their need to obtain help from others. An additional aspect related to the link between FA and fitness is that a low FA is 110 considered to be an attractive feature in many human populations (reviewed in 111 Johnston, 2006; Kościński, 2007; Little et al. 2011; Thornhill & Gangestad, 1999; Van 112 Dongen & Gangestad, 2011). 113

114

Another morphometric feature described as an indicator of fitness is the Waist-Hip Ratio (WHR), which results from dividing the waist perimeter by the hip perimeter. This measure is strongly influenced in women by hormone levels during puberty, which in turn determine the differential allocation of fat between sexes (Björntorp, 1997; Kirschner & Samojlik, 1991; Lev-Ran, 2001). Since the distribution of fat is very different between males and females, WHR can be considered as a secondary sexual characteristic in women. The standard values of WHR in Caucasian female populations

range from 0.67 to 0.80 (Marti et al. 1991). WHR is associated with both health and 122 fertility. Women with ratios around 0.70 present optimal oestrogen levels (Jasieńska et 123 al. 2004) and are less likely to develop serious illness, such as diabetes, cardiovascular 124 disorders and ovarian cancer (reviewed in Singh, 2002). Regarding fertility, women 125 with values of WHR of 0.80 or higher have significantly lower pregnancy rates than 126 women with lower values, independently of their Body Mass Index (Singh, 2002). In 127 128 addition, it has been pointed out that women with a low WHR present an ideal fat distribution in terms of fertility (Swami & Tovée, 2007). The link of this feature to 129 fertility and resistance to illness is to be expected, given that secondary sex 130 131 characteristics are linked to fitness in many species (Møller & Alatalo, 1999). 132 WHR is related to another physiological indicator of health in humans, the Body 133 134 Mass Index (BMI) (Flegal et al. 2013; Tovée et al. 1998, 1999), also linked to reproductive potential. Extreme values of BMI have a negative impact on fertility 135 (Brown, 1993; Kaplan, 1990; Lake et al. 1997; Reid & VanVugt, 1987). Given its 136 association with both health and fertility, many researchers have proposed BMI as a 137 primary measure of female attractiveness (Tovée et al. 1999), although it is commonly 138 recorded as a nutritional marker. The World Health Organization considers the range 139 18.50-24.99 as standard for adults. Values under 18.50 are considered underweight, 140 between 25 and 30 as overweight, and equal to or above 30 as obese. 141 142

Both WHR and BMI are important indicators of female attractiveness. Although 143 related, they display relatively independent effects. Controlling for BMI, women with a 144 WHR around 0.70 are classified as the most attractive by men of most cultures, 145 including Western Caucasian societies (Singh et al. 2010). Still, the optimal value in 146

terms of attractiveness ranges from 0.60 to 0.80 across different human populations
(Dixson et al. 2007; Marlowe et al. 2005). Individuals exhibiting a remarkable deviation
in their WHR (for example, women with high WHR and men with low WHR) are
commonly seen as less attractive by the opposite sex (Pazhoohi & Liddle, 2012). BMI
also influences individual attractiveness. Low values within the standard range, i.e.
around 20, are those typically regarded as more appealing (Tovée et al. 1998, 1999).

Another variable related with both phenotypic quality and attractiveness is the 154 degree of facial sexual dimorphism. Facial Femininity (FF henceforth) in women 155 156 positively correlates with disease resistance (Thornhill & Gangestad, 2006), oestrogen levels and fertility (Law Smith et al. 2006). Some authors have proposed FF as an 157 individual indicator of the historical energy balance and the capacity to allocate energy 158 159 for reproduction (Gangestad & Scheyd, 2005). Sexual dimorphism in facial features depends on sexual hormones levels during puberty (Johnston, 2006). Sexual 160 development in female faces entails certain noticeable modifications, such as thickening 161 of the lips and thinning of the cheekbones (Johnston, 2000). Hormone levels in puberty 162 (Berenbaum & Beltz, 2011) and, more specifically, the degree of masculinity/femininity 163 164 of the face, have proven to have an effect on adult behavior (Apicella et al. 2008; Carré et al. 2009; Haselhuhn & Wong, 2012; Pound et al. 2009; Stirrat & Perrett, 2010, 2012), 165 although most of these studies have been performed in men. More importantly, the 166 degree of masculinity/femininity has been described as a good predictor of 167 attractiveness both in women and men (reviewed in Johnston, 2006; Kościński, 2007; 168 169 Little et al. 2011; Thornhill & Gangestad, 1999).

Attractiveness affects human behavior both in individuals' everyday life and in 171 172 the laboratory (e.g., Langlois et al. 2000; Mulford et al. 1998; Takahashi et al. 2006; Wilson & Eckel, 2006). This could bring up a potential confound: the observed effects 173 of attractiveness-related features on behavior may operate directly or indirectly, that is, 174 by determining perceived attractiveness which subsequently affects behavior. In order to 175 control for this possibility, we included a score of self-perceived attractiveness (SPA 176 henceforth) as an additional variable. The effect of SPA on cooperation has already been 177 explored. Results show that women who find themselves attractive are less cooperative 178 in the PDG (Mulford et al. 1998). In general, individuals who consider themselves 179 180 attractive are also considered as such by others (Feingold 1992; Marcus & Miller, 2003; Weeden & Sabini, 2007). Hence, the SPA score allows us to test whether the fitness-181 related variables we consider influence cooperative behavior directly or through their 182 183 effect on self-perceived attractiveness.

184

Our main hypothesis is that women who display features associated with higher 185 fitness -low FA, high FF and low WHR- cooperate less often in the PDG. We base this 186 hypothesis on previous results indicating that men showing higher fitness are less prone 187 188 to behave pro-socially (Holtzman et al. 2011; Sanchez-Pages & Turiegano, 2010; Zaatari & Trivers, 2007; Zaatari et al. 2009). The standard explanation for these results 189 is based on the idea that cooperative behavior is a tool to receive future help from 190 others. Thus, high fitness individuals, who enjoy a greater capacity to obtain resources 191 by themselves, need to resort to cooperative behavior less often (Zaatari & Trivers, 192 2007). According to our hypothesis, women with a low WHR (controlling for BMI) and 193 a high FF should show less cooperative behavior in the PDG. We also expect to find a 194 positive effect of FA on cooperation, meaning that we expect symmetric women to 195

cooperate less often. This result has already been found for males (Sanchez-Pages &
Turiegano, 2010), and there is no reason to expect the influence of FA on behavior to be
sex-dependent.

199

We are also interested in whether the effects of these variables on cooperation 200 are mediated by attractiveness. One plausible hypothesis might be that these features 201 202 solely influence cooperative behavior through attractiveness because high-fit individuals are perceived as more attractive and also feel more attractive themselves. This can be 203 very important since attractive people tend to receive benefits from others without the 204 205 expectation of costly reciprocation. Under this hypothesis, the attractiveness of high fit individuals accustoms them to receive benefits which lead them to behave less 206 prosocially. In the present study, we can examine this hypothesis by analyzing whether 207 208 the effect of FA, WHR and FF on cooperative behavior depends on SPA. Still, we conjecture that these variables do not exclusively operate through attractiveness. This is 209 210 because high fit individual is more capable of obtaining resources independently of whether they receive them from others who consider her as attractive. So, as a second 211 hypothesis, we postulate that all these three features exert their effect on cooperation 212 213 independently of SPA. Such result would imply that the biological determinants behind the studied features (such as developmental stability and hormone levels) wield their 214 influence on behavior regardless of whether the individual considers herself as attractive 215 216 or not.

217

### 218 **2.0 METHODS**

219 - 2.1 Design and performance of experiments

Experiments were performed at the Faculty of Sciences of the UAM (Madrid, Spain). Participants were recruited among the student population few weeks before the semester exams in the spring and autumn of 2012. Recruitment was made by means of advertisement billboards and e-mail (sent by non-teaching staff) as the UAM ethical committee requires. In total, 176 White Spanish females took part in this study.

226

Participants played the PDG within a set of different tests (not considered in the 227 current paper). In the PDG, subjects have to choose between two possible strategies: 228 "cooperate" or "defect". If the two players choose "cooperate" they both get 90 points, 229 if both choose "defect" each one gets 30 points. If they choose different actions, the one 230 231 who cooperates gets 10 points and the one who defects obtains 160 points. The 232 exchange rate used in the experiment was 100 points = 1€. Under the standard gametheoretical approach "defect" is a dominant strategy because it is the strategy that 233 maximizes the individual benefit regardless of the decision of the counterpart. In 234 235 addition to playing the PDG, participants were asked to guess the decision of their opponent (Expected Behavior, EB). This variable has been shown to be a strong 236 determinant of behavior in the PDG (Sanchez-Pages & Turiegano, 2010). Participants 237 played a single round of the PDG. They were informed that they were playing against 238 another female participant from a previous session. They did not know anything else 239 about their counterpart. Subjects knew that their decisions would affect participants of a 240 241 future session in the same way. The experiment was run employing the Z-Tree 3.2.10 242 software (Fischbacher, 2007). Each participant was allocated a computer terminal. Experimental sessions had less than 20 subjects each. Participants received a show-up 243 fee (5€) and a variable reward dependent upon the decisions taken in the different 244

games implemented in the experiment. Final payment was 13.25±0.08€ (av±SEM) per
person (PDG average payment was 0.87±0.04€). Prior to the experiment, participants
were informed that their final payment would depend upon their decisions in several
items of the study, but not in all of them. Few weeks after the experiment, subjects were
informed about the exact payment procedure.

At the end of each experimental session, pictures of each participant were taken to prospectively measure individual FA and FF. Their height, weight, and both waist and hip perimeter were measured in order to estimate BMI and WHR. Participants also provided some personal data by filling up a questionnaire (age, current studies, ethnic group, sexual orientation, SPA). All data remained completely anonymous as required by the ethical committee of the UAM.

256

### 257 - 2.2 Measurement of morphometric variables

258

Three full frontal facial color photographs were taken of each participant, at 259 three meters of distance and under standardized light conditions with the zoom 260 completely opened in order to avoid distortion of the facial shape. Participants were 261 262 asked to remove any facial adornment, to pose with a neutral expression and to look directly into the camera. To measure FA from these images, the shape of each face was 263 defined by manually setting 39 predetermined Landmarks (LMs). These 39 points can 264 be unambiguously identified in each photo (Figure 1). The LMs were placed twice by 265 two of the authors in order to detect possible placement errors. LMs were located 266 employing the TPS software (by FJ Rohlf, available at 267 http://life.bio.sunysb.edu/morph/) 268

269

To calculate the FA of each image, we compared the LMs of each face and its 270 mirror-image (Klingenberg et al. 2002). The asymmetry of a bilateral object can be 271 partially attributed to directional asymmetry (differences in the population between 272 average right and left size) and partially to FA (deviation of each individual's asymmetry 273 from the overall average asymmetry). We obtained FA by decomposing the Procrustes 274 distance between each image and its mirror-image using the Procrustes ANOVA method 275 276 (Klingenberg & McIntyre, 1998). This decomposition was performed with the Morpho J software (available at http://www.flywings.org.uk/MorphoJ page.htm). As an individual 277 measure of symmetry we used the Mahalanobis distance, which avoids the effect of 278 279 correlation between variables (Rodríguez-Salazar et al. 2001). We thus employed a value of FA that is highly independent of the selected LMs. To control for the potential 280 error in the LMs placement, FA computation in Morpho J requires two sets of LMs for 281 282 each face (each set placed by a different researcher). Error in LM positioning was not significant (Procrustes ANOVA, error SS=9,297 x 10<sup>-3</sup>, df=13172, F=0,006, p=0.989). 283 284

We estimated Facial femininity (FF) by measuring the Procrustes distance between each participant's average face and a masculine reference face. The masculine reference face was built from the images of 100 males belonging to the same age and population as the subjects of study. Participants' average face was obtained as an average of the three captured pictures and their mirror-images. The use of symmetrical average faces for comparison with the masculine reference face avoids any undesired effect of individual symmetry in the measure of FF.

292

We computed the WHR by dividing the waist perimeter by the hip perimeter of each participant and trying to minimize the error caused by clothes. Waist perimeter was

295	measured in the lower girth region of the natural waist, generally right above the
296	umbilicus. Hip perimeter was measured in the wider point of the gluteus. During
297	measurements, participants stood feet together, loosen arms, normal breath, and with
298	their body weight uniformly distributed. In order to estimate BMI, the weight and height
299	of each participant was measured barefoot and without heavy clothing. A female
300	researcher took these measurements from each participant privately and just once.
301	
302	- 2.3 Self-perceived Attractiveness (SPA)
303	
304	To obtain SPA, each participant reported an estimation of its own attractiveness
305	in a 1 to 7 Likert-like scale, being 1 the lowest score and 7 the maximum, assessed as
306	deviations of the population average. Participants who consider themselves on the
307	average were advised to score themselves with 4.
308	
309	- 2.4 Statistical analyses
310	
311	We tested for the normality of all variables by means of the Shapiro-Wilk test.
312	For those variables not normally distributed, we performed the usual logarithmic
313	transformations. However, both SPA and BMI were resistant to that transformation. To
314	analyze the results, we employed (non-parametric) Spearman Rho ( $\sigma$ ) for correlations,
315	two-tailed Student-t tests for the normally distributed variables and Mann-Whitney test
316	for SPA and BMI. We also employed logistic regressions to analyze the simultaneous
317	effect of several variables on our dichotomous dependent variable ("Cooperate" or
318	"Defect"). We employed SPSS 15.0 (SPSS Inc.) in all the statistical analyses.
319	

320 <u>3.0 RESULTS</u>

321

Table 1 presents the summary statistics of all the variables considered. First, we 322 analyzed how the physiological variables relate to SPA. As expected, SPA correlates 323 negatively with WHR, BMI and FA (Table 2). Although our measure of FF did not 324 correlate with SPA, it negatively correlates with WHR. This is quite remarkable given 325 that both features are strongly influenced by hormone levels during puberty. Age did not 326 correlate with any of the morphometric variables or with SPA, although it must be noted 327 that the age range of our subjects was very narrow. Although WHR and BMI do not 328 329 show a significant correlation in our data, we followed the literature and controlled for BMI in any further analysis including WHR. 330

331

332 Regarding behavior in the PDG, 31.30% (n=55) of the 176 participants did not cooperate, a fraction consistent with results previously observed in the literature. We 333 also tested for differences in behavior according to the expectation that participants had 334 on the behavior of their counterpart. There was a strong and significant association 335 between the behavior of a participant and the behavior she expected from her 336 counterpart ( $\gamma^2 = 42.718$ , p<0.001). Of the participants who expected their counterpart to 337 cooperate (n=123), 83.74% (n=103) of them cooperated, whereas of the other 53 338 participants who expected their counterpart to defect, 66.04% (n=35) defected. 339

340

Next, we analyzed the relationship between behavior in the PDG (cooperate or defect) and the individual variables considered (Table 1). Results reveal that those subjects who defected displayed a higher WHR and a lower FA than those who cooperated. In addition, and in line with the literature, participants who defected

perceived themselves as attractive (high SPA). Age, FF and BMI were not significantlydifferent between participants who cooperated and those who defected.

347

We performed a set of logistic regressions in order to test simultaneously the 348 effect of these variables on cooperation in the PDG (Table 3). In an initial analysis, we 349 included all the morphometric variables plus Age (first row of Table 3). We observed 350 351 that WHR and FA were statistically significant. Note that the coefficients associated to these variables are negative and positive respectively. In other words, participants with 352 low WHR and high FA tended to cooperate more in the PDG. Next we built a simpler 353 354 model excluding Age and FF given that they were not significant (second row of Table 3). In this model, the variables FA and WHR remained significant. In the following 355 model (third row of Table 3) we included the variable SPA (which correlates with both 356 357 WHR and FA) in order to test whether the effect of the morphometric variables on the decision in the PDG depends on how attractive participants find themselves. In that 358 model, all SPA, WHR and FA were significant. High values of SPA and WHR led to 359 defection, whereas high values of FA led to cooperation. Hence, the physiological 360 variables FA and WHR remained significant after including SPA in the logistic 361 362 regression model. It is remarkable that both a low SPA and a low WHR relate with a tendency to cooperate considering that WHR negatively correlates with attractiveness. 363 Women who see themselves as relatively unattractive cooperate more often, but women 364 with low WHR –an attractive feature- tend to be more cooperative as well. 365

366

Finally, we included the variable Expected Behavior (EB) which has been
described to strongly affect participants' decision in the PDG (fourth row of Table 3).
The resulting model confirmed this finding: When participants expected their

counterpart to cooperate, they were more inclined to cooperate. It is worth noting that 370 371 the significance of FA and SPA barely changed after the inclusion of EB. This result suggests that the effect of FA and SPA on behavior in the PDG does not operate through 372 EB. However, the inclusion of EB in the model rendered WHR non-significant at the 373 95% confidence level. This leads us to conclude that the effect of WHR on cooperation 374 operates mostly through its influence on the expectation that subjects hold on the 375 376 behavior of their counterpart. In fact, there were no significant differences in FA ( $t_{174}$ =-1.104; p=0.312) nor SPA (U=3001.5; N<sub>1</sub>=53, N<sub>2</sub>=122; p=0.374) between those who 377 expected their counterpart to cooperate and those who expected the opposite. But there 378 were significant differences in WHR between the two groups ( $t_{174}=2.519$ ; p=0.013): 379 those participants who expected their opponent to cooperate displayed lower ratios 380  $(0.715\pm0.004)$  than those who expected defection  $(0.732\pm0.006)$ . 381

382

### 383 **<u>4.0 DISCUSSION</u>**

384

The goal of the present study is to analyze the existing relationship between cooperative behavior in women and a set of individual characteristics previously categorized as indicators of phenotypic quality (high fitness), that are also known to be related with female attractiveness.

389

Of the studied variables, FA and WHR showed an effect on the decision to
cooperate. Even more interestingly, and in line with our second hypothesis, their effect
seems to be independent of the perception that individuals have of their own
attractiveness. This is shown by the fact that FA and WHR maintained their significance
after controlling for SPA, This independent effect of the physiological variables and

SPA on participants' cooperative behavior in the PDG is undoubtedly the moreoutstanding result of our study.

397

Several studies reveal an association between behavior and fitness related 398 features, particularly symmetry, in humans (Furlow et al. 1998; Manning & Wood, 399 1998; Muñoz-Reyes et al. 2012; Pound et al. 2007), and more specifically in relation to 400 401 cooperative or prosocial behavior (Holtzman et al. 2011; Sanchez-Pages & Turiegano, 2010; Zaatari & Trivers, 2007; Zaatari et al. 2009). Nevertheless, to date, no study had 402 explored whether the effect of symmetry (or other physiological variables) works 403 404 through the self-perception of personal attractiveness. A plausible explanation of the observed effect of FA on cooperative behavior might be that a symmetric person should 405 feel more attractive and, therefore, more entitled to obtain resources autonomously due 406 407 to the benefits conferred by attractiveness (reviewed in Langlois et al. 2000; Mulford et al. 1998). Our results, however, cast doubts on this explanation. The effect of FA on 408 cooperation is independent of the effect of self-perceived attractiveness given that the 409 effect of phenotypic quality on women's behavior remains significant after controlling 410 for self-perception of attractiveness. While remarkable, the independent effect of these 411 412 two factors is not entirely unexpected. Results observed in studies with males reveal that although men who find themselves attractive tend to cooperate more (Mulford et al. 413 1998, but see Takahashi et al. 2006), highly symmetrical males cooperate less often 414 (Sanchez-Pages & Turiegano, 2010). This occurs even though attractiveness and 415 symmetry are correlated (reviewed in Johnston, 2006; Kościński, 2007; Little et al. 416 2011; Thornhill & Gangestad, 1999; Van Dongen & Gangestad, 2011). The basis of this 417 intriguing relationship between FA and behavior, triggered independently of SPA, could 418 be explained by an unconscious self-adjustment of behavior to its expected 419

consequences based on previous experience. It has been described that several animal 420 421 behaviors adjust to mathematical models based on their cumulative rate of success and failure despite animals do not use such models consciously (Dugatkin & Reeve, 2000). 422 The link between symmetry and a low tendency to cooperate might be due to other 423 individual characteristics which could be associated to FA, such as self-confidence or 424 perceived self-sufficiency (the estimation of the own ability to obtain resources). As a 425 426 matter of fact, symmetry is correlated with several personality traits, like neuroticism, agreeableness and openness to experience, the last two negatively (Fink et al. 2005; 427 Holtzman et al. 2011). This association might be behind the link we observe between 428 429 low FA and a weaker tendency to cooperate. Even though we find these questions quite interesting, they are beyond the scope of this study. 430

431

432 Independently of the mechanism behind it, the link we find between FA and cooperative behavior in women is to be expected given the results already found in men. More 433 symmetrical males are less pro-social in the PDG (Sanchez-Pages & Turiegano, 2010) 434 and in the UG (Zaatari & Trivers, 2007), and display fewer pro-social personality traits 435 (Holtzman et al. 2011). Considering their higher phenotypic quality (Thornhill & 436 437 Gangestad, 2006), low FA individuals depend less on maintaining a good relationship with their social environment, and, hence, are not prone to sacrifice personal benefits in 438 order to favour others (Zaatari & Trivers, 2007). This explanation (already proposed in 439 Mulford et al. 1998) also fits with the relationship between attractiveness and 440 cooperative behavior described in this paper under the hypothesis that attractiveness is a 441 valid indicator of fitness (Langlois et al. 2000). We do not want to imply that the need 442 for resources was behind participants' behavior in our experiment. We rather suggest 443 that their different capabilities in obtaining resources and their experiences when 444

sharing them might have shaped subjects' daily behavior and made them more or lesspro-social independently of their short-term needs.

447

The independence between the effects of attractive-related physiological features and of 448 SPA is evident in the case of WHR (once controlled for BMI). Even though low WHR 449 scores are associated with attractiveness in women (Singh et al. 2010), we show that 450 451 low WHR values associate with cooperative behavior. This result is unexpected if one exclusively focuses on the relationship between WHR and attractiveness. It confirms 452 our conclusion that the effect of the attractive-related variables on cooperation does not 453 454 operate exclusively through their influence on SPA. A likely explanation for this result stems from the positive association we found between a high WHR and the belief in the 455 defection of the opponent. The effect of WHR on EB seems to be the strongest 456 457 determinant of participants' behavior; Table 3 shows that EB explains individual behavior in the PDG better than any other variable (also in Mulford et al. 1998; 458 Sanchez-Pages & Turiegano, 2010). That is, a high WHR is associated with a tendency 459 to believe that the opponent will not cooperate, and this belief leads to defection. The 460 relationship we observe between high WHR and the belief on the counterpart's 461 462 defection is to be expected, especially given the associations already described in healthy women between this variable and different distrustful behaviors, such as 463 hostility (Kaye et al. 1993), low self-perceived social status (Adler et al. 1993), and 464 social anxiety (Landén et al. 2004). This may suggest that WHR, beyond of its 465 relationship with fitness (Jasieńska et al. 2004; Singh, 2002; Swami & Tovée, 2007), 466 may be indicating 'desirability as a social partner' which, in turn, leads to women 467 showing higher values (low desirability) to behave distrustfully in social interactions 468 because of their previous experiences. 469

471	The FF of the participants had no significant effect on the propensity to
472	cooperate in the PDG. Although the degree of sexual differentiation of the face has a
473	well-known association with several behaviors, to date, most of the studies on this issue
474	have focused only in men (Apicella et al. 2008; Pound et al. 2009; Stirrat & Perrett,
475	2010, 2012). These studies employ the ratio between facial width and height (both in
476	men and women) as a measure of masculinization/feminization. This feature was
477	initially described as dimorphic between sexes (Carrè & McCormick, 2008; Weston et
478	al. 2007), but has recently been questioned as such (Kramer et al. 2012; Lefevre et al.
479	2012). In any case, in studies which included female participants, this measure of
480	masculinity (or femininity) showed no effect on the propensity to engage in deception
481	or cheating during a negotiation (Haselhuhn & Wong, 2012), nor in dominance (Carrè &
482	McCormick, 2008). However, the same measure showed an effect on male behavior
483	under the same experimental conditions. Therefore, our results are consistent with those
484	stating that facial sexual dimorphism may influence behavior in men but not in women.
485	It might be argued that we are not measuring facial femininity properly, but the strong
486	correlation between FF and WHR substantiates the robustness of our femininity
487	measure (see Table 2). This correlation is in line with the relationship previously
488	observed between facial and body attractiveness when measured separately, which
489	confirms that these two variables are valid indicators of fitness (Thornhill & Grammer,
490	1999). Although both FF and WHR are related to oestrogen levels, it is remarkable that
491	they do not have the same effect on cooperative behavior. This fact suggests that
492	considering the stage of development in which the feminizing effect of hormones occurs
493	is important in order to ascertain its effects on a specific behavior. Obviously, additional

494 experiments and physiological studies are needed to deepen our understanding of this495 result.

496

Regarding our first hypothesis, of the three variables related to fitness, only FA 497 displayed the expected effect on cooperation, while FF showed no effect and WHR 498 vielded the opposite. However, the effect of SPA fits with our hypothesis if one 499 considers it as a reliable signal of fitness (Langlois et al. 2000). In summary, two 500 variables confirmed our expectations and two did not. It is very interesting that WHR 501 and FA, which are strongly correlated (see table 2) and linked to fitness, have opposite 502 503 effects on cooperative behavior. The strong correlation between them and their correlation with SPA confirm them as measures of phenotypic quality, like facial and 504 body attractiveness (Thornhill & Grammer, 1999), facial and voice femininity (Feinberg 505 506 et al. 2005) and symmetry and sexual dimorphism (Little et al. 2008). The fact that their effects on behavior in the PDG follow different directions suggests that they relate to 507 508 different kinds of high-fit features (Gangestad & Scheyd, 2005; Singh, 2002; Swami & Tovée, 2007; Van Dongen & Gangestad, 2011). That aside, this contradiction also casts 509 doubts on the idea that the motivation to cooperate is only related to the possibility of 510 511 obtaining resources from others through reciprocation. This is only one of the possible, and not mutually exclusive, motivations of pro-social behavior (social norms and ethical 512 beliefs are also obvious factors). The mixed results obtained here demonstrate the 513 difficulty of associating any behavior to a single motivation. 514

515

Let us remark that the present study is one of the few analyzing pro-social behavior solely in women. In a public good game played only by females, Buser (2012) found that contributions were higher during the menstrual phase of the menstrual cycle

and that those participants with a lower 2D:4D ratio contributed less. Nevertheless, 519 520 there exists a vast literature comparing behavior between men and women in strategic games (reviewed in Balliet et al. 2011). Results show consistently that men and women 521 act differently depending on the sex of their counterpart in social dilemmas. The lowest 522 levels of cooperation are usually found in setups where only women participate. While 523 in mixed-sex interactions women tend to be more cooperative, men tend to be more 524 525 cooperative in same-sex interactions (Baillet et al. 2011; Croson & Gneezy, 2009). Under an evolutionary perspective, these differences are usually attributed to the 526 advantage of males when forming coalitions aimed to obtain resources in hunting and 527 528 war. This difference between men and women could in turn mediate the effect of SPA, 529 WHR and FA when women face mixed-sex instead of single-sex strategic interactions.

530

To conclude, and beyond the interest of the results obtained and their 531 532 implications, it is important to remark that this study, as many others, was performed using exclusively a university population within a western culture. For this reason, 533 before generalizing results to the human species, it would be needed to extend the 534 experiments to a major range of ages and socio-cultural strata, including a wider range 535 of ethnicities. This is particularly necessary when considering WHR given that its 536 association with numerous features relies partially on the ethnicity of the subjects (Kaye 537 538 et al. 1993). However, we can conjecture what could be the effect of fitness related variables on cooperative behavior in non-western industrialized societies. As it has been 539 described (Henrich et al. 2010), people in many of these societies behave more in line 540 with the predictions of Standard Game Theory. Following this pattern, one should 541 expect less people to cooperate in the PDG in non-industrialized societies. Therefore, 542

543	under the assumption that cooperative behavior is a tool to receive future help from
544	others, only extremely low-fit individuals (showing remarkable unadaptative values in
545	these variables) should cooperate often in these societies. Of course, this can only be
546	elucidated by performing comparable experiments in other societies.
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# 765 Tables and figures766

- Table 1: Summary statistics for the entire subject population and according to choice in
- the PDG.

769 (Mean  $\pm$  SEM. For statistics analysis, the natural logarithm of WHR was employed).

	TOTAL	Defect (n = 55)	Cooperate (n = 121)	
Age (yr)	$21.42\pm0.19$	$21.31 \pm 0.31$	$21.48 \pm 0.24$	$t_{174} = -0.419; p = 0.675$
WHR	$0.7198 \pm 0.003$	$0.7300\pm0.006$	$0.7152 \pm 0.004$	$t_{174} = 2.184; p = 0.030$
BMI	$22.746\pm0.291$	$23.294\pm0.592$	$22.497 \pm 0.326$	U = 3000; N <sub>1</sub> = 55 N <sub>2</sub> = 121; p = 0.296
FA	$4.248 \pm 0.038$	$4.101\pm0.065$	$4.3155 \pm 0.046$	$t_{174} = -2.631; p = 0.009$
FF	$8.318 \pm 0.131 \ x \ 10^{-2}$	$8.238\pm0.204$	$8.354\pm0.166$	$t_{174} = -0.412; p = 0.681$
SPA	$4.313 \pm 0.071 \qquad 4.564 \pm 0.132 \qquad 4.198 \pm 0.08$		$4.198 \pm 0.083$	U = 2666.5; N <sub>1</sub> = 55 N <sub>2</sub> = 121; p = $0.024$
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	LN [WHR]	BMI	FA	FF	Age	
SPA	$\sigma_{176} = -0.255$ p = 0.001	$\sigma_{176} = -0.190$ p = 0.011	$\sigma_{176}$ = -0.178 p = 0.018	$\sigma_{176} = -0.070$ p = 0.357	$\sigma_{176} = 0.084$ p = 0.265	
	LN [WHR]	$\sigma_{176} = 0.118$ p = 0.119	$ \sigma_{176} = 0.235  p = 0.002 $ $ \sigma_{176} = -0.217  p = 0.004 $		$\sigma_{176} = 0.027 \\ p = 0.720$	
		BMI	$\sigma_{176} = 0.106$ p = 0.162	$\sigma_{176} = -0.129$ p = 0.087	$\sigma_{176} = 0.117$ p = 0.124	
			FA	$\sigma_{176} = -0.046$ p = 0.546	$\sigma_{176} = 0.040$ p = 0.602	
				FF	$\sigma_{176} = 0.042$ p = 0.577	

Table 2: Spearman Rho correlation between considered variables

- Table 3: Estimation of the probability of cooperation in the PDG: Logistic models.
- 776 (Expected Behaviour of the opponent (EB) was coded as 1 if cooperation was expected

Variables in	MODEL			VARIABLE					
the model	-2LL	Likelihood Ratio Test	df	р	variables	coef	Wald	df	Р
	202.882	15.741	5	0.008	Constant	-7.246	5.657	1	0.017
$\mathbf{L}_{\mathbf{n}}(\mathbf{W} \mathbf{I}\mathbf{D})$					Ln(WHR)	-8.394	6.008	1	0.014
DML EA					BMI	-0.023	0.229	1	0.632
EF Age					FA	1.137	9.551	1	0.002
II, Age					FF	-0.113	0.001	1	0.991
					Age	0.048	0.467	1	0.494
				0.002	Constant	-6.210	5.951	1	0.015
Ln(WHR),	203.360	15 262	3		Ln(WHR)	-8.284	6.043	1	0.014
BMI, FA		13.262			BMI	-0.020	0.176	1	0.675
					FA	1.125	9.475	1	0.002
	191.849 26.773 4	849 26.773	4	<0.001	Constant	-3.089	1.263	1	0.261
SPA,					SPA	-0.715	10.410	1	0.001
Ln(WHR),					Ln(WHR)	-11.407	9.736	1	0.002
BMI, FA					BMI	-0.056	1.280	1	0.258
				FA	1.085	8.194	1	0.004	
	, 157.962 60.660			5 <0.001	Constant	-2.776	0.754	1	0.385
ED CDA					EB	2.293	29.791	1	< 0.001
ED, SPA, $I_{p}(W \sqcup P)$		60 660	5		SPA	-0.671	7.572	1	0.006
$\frac{\text{LII}(\text{WIIK})}{\text{RMI FA}}$		00.000	3		Ln(WHR)	-7.649	3.414	1	0.065
Divi1, 171					BMI	-0.096	2.865	1	0.091
					FA	1.127	6.315	1	0.012

and 0 if defection was expected.)

780 Figure 1: Example of landmarks placement.

