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Socioeconomic position, immune function, and its physiological markers

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ABSTRACT

The development of costly traits such as immune function and secondary sexual traits is constrained by resource availability. The quality of developmental conditions and the availability of resources in ontogeny may therefore influence immune system functions and other biological traits. We analyzed causal pathways between family socioeconomic position, strength of immune response, and five physiological biomarkers in young Latvian men ($n = 93$) using structural equation modeling. Men from wealthier families had higher testosterone levels ($r_s = 0.280$), stronger immune response ($r_s = 0.551$), and higher facial attractiveness ($r_s = 0.300$). There were weak, non-significant correlations between family income, body fat percentage ($r_s = -0.147$), and fluctuating asymmetry ($r_s = -0.159$). Testosterone partially (33.8%) mediated the effect of family income on facial masculinity. Testosterone (positively) and adiposity (negatively) partially (4%) mediated the relationship between family income and immune function. Higher facial masculinity, higher facial symmetry, and lower adiposity were reliable and independent cues of better immune function ($R^2 = 0.238$) in a larger sample of young Latvian men ($N = 146$). Resource availability in ontogeny has an important role for the development of immune function and physical appearance, and it is a key parameter to be included in human eco-immunological research.

1. Introduction

A highly developed immune system protects organisms from pathogens, parasites, and pathologies caused by the organism itself—however, having a highly developed immune system is energetically costly, and its development is traded off against other traits and activities (Roved et al., 2017), such as secondary sexual characteristics. In males, secondary sexual traits are hypothesized to be honest signals of mate quality (Folstad and Karter, 1992; Stephen and Luoto, 2021). According to the immunocompetence handicap hypothesis, lower immune responses in males compared to females result from the immunosuppressive effects of testosterone (Foo et al., 2020). This hypothesis has been supported by findings from 38 species (Foo et al., 2017). Therefore, only high-quality males with good genes can afford to display high-quality secondary sexual traits (Roved et al., 2017; Stephen and Luoto, 2021) whilst also being able to produce a robust immune response. The development of secondary sexual traits is dependent on testosterone, and on testosterone's interaction with cortisol (Adam et al., 2017;

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Rantala et al., 2012).

Resource availability in ontogeny may affect both the development of the acquired immune system and the development of secondary sexual characteristics (Krams et al., 2019), such as facial masculinity (Ekrami et al., 2021). Even minor variation in genetic, developmental, and physiological quality among males can be amplified to perceptible levels in secondary sexual characteristics (Luoto, 2019; Zaidi et al., 2019). Men's secondary sexual characteristics are attractive to women, and since these sexual preferences are heritable (Zietsch et al., 2015), they may comprise evolutionary adaptations whereby women use men's secondary sexual characteristics as cues for securing direct (e.g. bioenergetic investment) and indirect benefits (e.g., good genes) for their offspring from healthy, robust males (Luoto, 2019; Zaidi et al., 2019; Stephen and Luoto, 2021).

Evolutionary–developmental studies on costly traits can observe positive or negative correlations between the development of such traits depending on whether the bioenergetic tradeoffs between competing traits are more substantial than the total amount of resources that is available for their development (Krams et al., 2019; Lauringson et al., 2020; Rubika et al., 2020). For instance, facial masculinity is positively correlated with immune function when immune function is measured via the ability to produce antibodies in response to a novel antigen (in this case: vaccine) (Rantala et al., 2013). When using a genetic measure of immune function, facial masculinity does not reliably reflect this genotypic facet of male immunity (Zaidi et al., 2019). This indicates that focusing on genotype (as in Zaidi et al., 2019) is insufficient when analyzing individual differences in immune function, and the use of a more holistic suite of markers of immune function is preferable (Foo et al., 2020). In this study, we therefore focused on phenotypic markers of facial masculinity and immune function, which are also sensitive to developmental conditions (cf. Krams et al., 2019).

Besides these phenotypic measures, resource availability in ontogeny can influence the developmental stability of organisms, which may be reflected in individual differences in a number of physiological traits (Ellis and Del Giudice, 2019; Luoto et al., 2019a; Maner et al., 2017). Fluctuating asymmetry is the sum of random deviations from perfect symmetry in bilateral organisms (Gangestad et al., 1994). It is assumed that deviations away from perfect symmetry reflect the impact of developmental and environmental stress experienced by bilaterally symmetric organisms during their development (Beasley et al., 2013; Gangestad et al., 2010). Therefore, the bilaterally structured traits of an organism that has developed in a poor environment or experienced high levels of stress during ontogeny should have a greater degree of asymmetry than an organism that developed in a stable, resource-abundant environment. A meta-analysis of nonhuman animal studies found that fluctuating asymmetry is a sensitive biomarker of environmental stress: environmental stressors accounted for 36% of the variance in fluctuating asymmetry across studies (Beasley et al., 2013). Thus, fluctuating asymmetry is an important biomarker for evaluating the impact of stressors on individual development. Fluctuating asymmetry is not heritable (Blanckenhorn and Hosken, 2003), and it might be linked to resource availability and the strength of immune system (Gupta et al., 2016).

The exposure of developing organisms to environmental stressors may have several physiological consequences, including a decline in immune function. Mounting an immune response against a foreign antigen may itself constitute a cost (Krams et al., 2012, 2013). Immune responses to vaccines impair growth rate and developmental stability, also increasing fluctuating asymmetry in growing organisms (Prendergast and Humphrey, 2014), suggesting trade-offs between immune function and other energetically costly activities and traits. These trade-offs may depend on the availability of resources: vaccination, for example, results in a decreased ability to produce antibodies in individuals with limited access to resources (Krams et al., 2019). However, the links between fluctuating asymmetry and fitness-related traits such as sexual attractiveness and the ability to mount a novel immune response have never been tested based on their dependence on resource availability in humans.

There is a strong preference for symmetry in mate choice across species, and higher symmetry in facial and bodily parameters has been cross-culturally associated with physical attractiveness and beauty (Phalane et al., 2017; Stephen and Luoto, 2021). Higher facial and bodily symmetry have been considered as indicators of good health condition and genetic constitution (Gangestad et al., 2010; though see Stephen and Luoto, 2021). Facial attractiveness—but not facial symmetry—has been linked with more robust immune function in African men (Phalane et al., 2017).

We predicted that young men from families with a higher income have (1) lower adiposity (Maner et al., 2017), (2) lower facial fluctuating asymmetry, (3) higher facial attractiveness, and (4) more robust immune function (as in Krams et al., 2019; a subsample of the current sample). Although theoretically we remained agnostic about the relationship between family income and testosterone, recent research has suggested a causal influence of testosterone on income (Hughes and Kumari, 2019). Furthermore, both testosterone concentrations and life history strategies have a significant heritable component (Luoto et al., 2019a), so we expected (5) a positive relationship between family income and testosterone. We also predicted that (6) testosterone mediates the relationship between family income and facial masculinity. Both negative and positive relationships between testosterone and immune function have been previously reported; however, both positive and negative correlations can be interpreted as supportive of an immunosuppressive effect of testosterone (Foo et al., 2017). It is well known that obesity and fat mass impair immune function and that there is a bidirectional link between testosterone and adiposity (Francisco et al., 2018; Kelly and Jones, 2015; Rantala et al., 2013; a subsample of the present sample). We therefore expected that (7) testosterone (positively) and adiposity (negatively) mediate the effect of family income on immune function. Based on prior research (Phalane et al., 2017), we also predicted that (8) facial masculinity is a more reliable cue of immune function than facial asymmetry. We reanalyzed datasets from previous research on relationships between immunity, facial attractiveness, vocal attractiveness, height, adiposity, and family income (Krams et al., 2014, 2019; Rantala et al., 2013; Skrinda et al., 2014), updating datasets with more participants on family income, and including traits (facial asymmetry) and predictions that have not been analyzed before.

2. Method

2.1. Participants and facial photographs

We studied associations between family income, antibody titers against hepatitis B antigen, facial fluctuating asymmetry, and facial attractiveness in 146 young men (21.24 ± 1.44 years old, *mean* ± *SD*, range 19–25 years) in southeastern Latvia in 2010. Participants were students from Daugavpils University and Transportation College of Daugavpils. Full color facial photographs were taken with Nikon D50 and Nikon D5200 digital cameras under standardized lighting conditions with subjects having a neutral facial expression (Rantala et al., 2012, 2013).

We included only those participants ($n = 93$) in our family income analyses with (i) socioeconomic status known since their birth and (ii) those whose socioeconomic status was relatively constant over time. The existing data set was also restricted by participant lifestyles (no smoking until 16, no drugs, no serious diseases). None of the participants was dropped from the analyses because of serious disease, smoking, or drugs. Descriptive statistics for the dataset are given in Table 1.

2.2. Immune system assay

Hepatitis B is a serious viral infection that can cause both acute and chronic liver disease. This infection is transmitted through contact with

Table 1
Descriptive statistics for the data.

Variable	*n*	Min.	Max.	Mean	Std. error	Std. dev.
Immune function	146	0.0	73	6.28	0.857	10.35
Adiposity	146	5.6	34.8	14	0.484	5.848
Testosterone	146	4.0	30.0	13.41	0.395	4.771
Facial masculinity	146	0.2	6.2	3.37	0.102	1.235
Facial asymmetry	146	2.6	56.6	16.29	0.872	10.54
Facial attractiveness	146	-3.4	2.97	-0.62	0.138	1.665
Family income	93	1	7	2.86	0.139	1.34

the blood or other body fluids of an infected person. Hepatitis B can be prevented by safe and effective vaccines (Schönberger et al., 2013). We activated the immune system of the subjects using a safe and effective hepatitis B vaccine (Engerix-B, GlaxoSmithKline) (for more information, see (Krams et al., 2014; Rantala et al., 2012; Skrinda et al., 2014)). We collected venous blood in 6 ml vials to measure the presence of antibodies before the vaccination. This was done to ensure that none of the participants had hepatitis B-specific antibodies before the vaccination. We thus measured the ability of the acquired immune system to produce antibodies against a novel antigen (not the ability of the acquired immune system to deal with an antigen already encountered by it).[1] One month after the vaccination, we again collected 6 ml of venous blood to measure the antibodies produced in response to the vaccination. To determine serum hepatitis B surface antigen (anti-HBs) levels, we used the commercially available AxSYM® AUSAB® microparticle enzyme immunoassay (MEIA). Anti-HBs concentrations were expressed in mIU/ml. Mean intra-assay CV was 2.9%, the lower level of detection was 2 mIU ml^{-1} and the analytical range was 2–1000 mIU ml^{-1}. The range of anti-HBs in the sample was 0–73 mIU ml^{-1}. The participants were considered to develop seroprotection against hepatitis B virus if they produced ≥10 mIU ml^{-1} of anti-HBs.

2.3. Testosterone

Testosterone concentration was detected from 10 ml of venous blood collected approximately 30 min before a dose of hepatitis B vaccine (Engerix B, Glaxosmithkline) was administered. The second measurement of testosterone was done one month after the vaccination. Blood samples were collected between 9:30 and 11:00. Previous research has shown no effect of this collection time on individual differences in testosterone levels (e.g., Brownlee et al., 2005; Borráz-León et al., 2018, 2019, 2021). Testosterone levels were assessed using an in-house competitive chemiluminescent enzyme immunoassay with commercially available kits (Rantala et al., 2012). Serum samples were incubated for 60 min at 37 °C with an alkaline phosphatase-labeled reagent and polystyrene beads coated with polyclonal rabbit antibody. Unbound material was removed by centrifugal wash, and bound quantities were measured using a specific chemoluminescent substrate (a phosphate ester of adamantyl dioxetane). Immulite® 2000 Total Testosterone quality control samples were included to assess the assay reliability. Mean intra-assay CV was 9.7%, the method lower limit of detection was 0.69 nmol l^{-1} (manufacturer's standard: 0.3 nmol l^{-1} [1]) and the analytical range was 0.69–55.55 nmol l^{-1}. Testosterone levels were consistent pre- and postvaccination (Cronbach $\alpha = 0.91$) and we averaged the values for each participant.

[1] Besides acquired immunity, the other part of the immune system is the innate component, which developed earlier in evolution than acquired immune responses. The innate immune system consists of all the immune defenses that lack immunologic memory. Innate responses therefore remain unchanged however often an antigen is encountered (Delves and Roitt, 2000).

2.4. Adiposity

Each participant's body fat percentage was measured using Omron Body Composition Monitor BF500 between 8:00 and 9:30 AM. Participants did not consume any food before adiposity measurements.

2.5. Fluctuating asymmetry of faces

Six bilateral traits were used to calculate fluctuating asymmetry: the inner (L1 in Fig. 1) and outer (L2) corners of the eyes, cheekbones (L3), outer edges of the lower nose region (L4), corners of the mouth (L5) and jawbones (L6). The traits were measured using the open source ImageJ software version 1.42 (NIH, Bethesda, MD, USA) with an accuracy of 0.01 mm. The midpoints of each line were calculated using the following formula [(left point – right point/2) + right point].

In a completely symmetrical face, all of the midpoints are positioned on the same vertical line and the sum of all of the differences among the midpoints is zero. Increasing values are reflective of and proportional to increasing facial asymmetry (Borráz-León et al., 2017a, 2017b).

To ensure the reliability of fluctuating asymmetry measurements, intraclass correlation coefficients were computed using the calculated fluctuating asymmetry values from two different pictures of the same participant ($n = 146$; $r = 0.912$; $p < 0.0001$). The average between the two fluctuating asymmetry values for each individual was used for all future calculations (Borráz-León et al., 2017a, 2017b).

2.6. Facial masculinity

The images were rated for facial masculinity by 35 heterosexual Latvian men (mean age, 22.8; *SD* 3.2) and 30 heterosexual Latvian women (mean age, 20.5; *SD* 2.0). The female participants reported regular menstrual cycles and no use of hormonal contraception. The facial images were rated on a seven-point Likert scale (1 = not masculine, 7 = very masculine). Facial images were presented in random order. Inter-rater reliability was high for all ratings (all Cronbach αs >0.93). Masculinity values were averaged across raters for all ratings.

2.7. Facial attractiveness

Forty-two heterosexual Caucasian women reporting regular

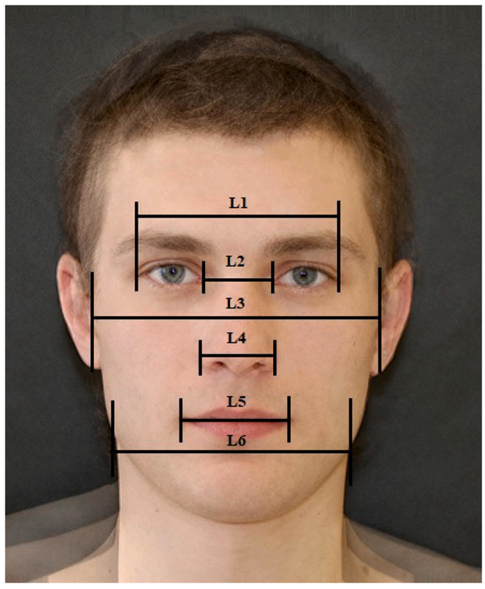

Fig. 1. A composite sample photo showing six bilateral traits used to calculate facial asymmetry. This sample photo represents the "average" face of young Latvian men. It is made by merging photos of 25 young men together.

menstrual cycles and no use of hormonal contraception from the University of Daugavpils, Latvia (mean age: 20.92 ± 0.98 years old, *mean* ± *SD*) rated the facial images for sexual attractiveness on an 11-point Likert scale (−5 = very unattractive, 0 = neutral and +5 = very attractive). The women were selected from a larger group of 122 women on the basis of being in the fertile phase of their menstrual cycle. The fertile phase was calculated as the 5 days preceding ovulation and the day of ovulation itself (Dunson et al., 1999). Ovulation was assumed to occur 14 days before the onset of menses. The method is commonly used in evolutionary psychological studies (e.g., Sohda et al., 2017). Images were presented in random order. Inter-rater reliability was high for all ratings (all Cronbach αs >0.94) and they were thus averaged across raters for all ratings.

2.8. Family income

There are several variables that characterize the socioeconomic status of an individual, such as age, education, job class, and income (often represented as annual household income of the individual: (e.g., Krams et al., 2019; Rubika et al., 2020; Tyrrell et al., 2016). The participants were 19–25-year-old men; all were undergraduate students with no job class achieved and with limited opportunities to work (none worked either before or during the study) because of their full-time studies. All of the participants lived with their parents during the study. Thus, with the exception of family income, all socioeconomic parameters of the subjects were similar. We interviewed the participants and their parents about current family income and family income since 1991 when most of the subjects were born. This is when Latvia regained its independence as a result of an economic crash and political crisis in the USSR.

We divided the time since 1991 into five periods and assigned each family into one of seven income categories. The statistical analyses were done based on recalled total family income divided by the number of family members. We included in the study only those families ($n = 93$) that remained in their income categories since 1991 or shifted away from the original socioeconomic status by a maximum of one category. In 2010, the first income group consisted of families with equivalent to or less than 50 EUR per family member/month; the second group, 50–100 EUR per family member/month; the third group, 101–150 EUR; the fourth group, 151–200 EUR; the fifth group, 201–250 EUR; the sixth group, 251–300 EUR; and the seventh group, 301–350 EUR. This division of income per family member/month corresponds to those traditionally used by Latvian economists and more recently by evolutionary anthropologists (Krams et al., 2019; Rubika et al., 2020).

In 2000, Latvia's population was 2.38 million people; in 2018, it was 1.89 million (United Nations, 2020). No other country has experienced a more precipitous fall in population during that period (Rubika et al., 2020; United Nations, 2020). The impact of Latvia's population crisis is severest and most evident in its poorest region, in the country's southeast corner bordering Belarus and Russia where this study was done. The average monthly wage in this region is about half of the average wage in Latvia (Central Statistics Office of Latvia, 2020). These factors created an environment where most of the participants were unable to improve their family income across decades (Krams et al., 2019).

2.9. Ethics statement

The study was approved by the Research Ethics Committee of Daugavpils University, Latvia (05/2012). All participants provided their written consent to participate in this study, and the ethics committee approved this consent procedure. The experiment was conducted according to the Declaration of Helsinki.

2.10. Statistical analyses

We used the nonparametric Spearman correlation analysis to test relationships between the study variables: family income, testosterone, adiposity, antibody titers of hepatitis B antigen (immune function), facial asymmetry, facial masculinity, and facial attractiveness. We performed two mediation analyses using structural equation modelling (SEM). In bootstrap analyses (10,000 bootstrap samples), mediation was considered significant if the 95% bias-corrected confidence intervals for the indirect effect did not include 0. In addition, we constructed a theory-driven structural equation model which included all of the seven variables measured in this study. The immune function variable was Box-Cox transformed ($x + 1, \lambda = -0.225$), while testosterone, adiposity, and facial asymmetry were log-transformed to improve normality of residuals. We used the Maximum Likelihood estimation method and evaluated the fit of the SEM using several diagnostic metrics: the chi-square test, the root mean square error of approximation (RMSEA), and the comparative fit index (CFI). A good model fit was inferred when chi-square p-value was >0.05, the RMSEA value was <0.1, and CFI was ≥0.90. Standardized path coefficients and model fit index values were calculated using SPSS AMOS.

3. Results

3.1. Bivariate correlations

We found a weak, non-significant correlation between family income and adiposity ($r_s = -0.147$, $p = 0.160$, $n = 93$; Fig. 2) and between family income and facial asymmetry ($r_s = -0.159$, $p = 0.129$, $n = 93$; Fig. 2). Predictions 1 and 2 were therefore not supported by the data, though the correlations were in the predicted direction in both cases. As predicted, there were significant correlations between family income and facial attractiveness ($r_s = 0.300$, $p = 0.003$, $n = 93$; Fig. 2), between family income and strength of immune response ($r_s = 0.551$, $p < 0.001$, $n = 93$; Fig. 2), and between family income and testosterone ($r_s = 0.280$, $p = 0.007$, $n = 93$; Fig. 2). Predictions 3, 4, and 5 were therefore supported by the data.

3.2. Mediation analysis: family income, testosterone, facial masculinity

There were significant bivariate correlations between family income and testosterone, testosterone and facial masculinity, and family income and facial masculinity (Fig. 2). To test prediction 6 about the mediating effects of testosterone on facial masculinity, we performed a mediation analysis with these variables entered into a SEM model. The change from the total effect (c path) of family income to facial masculinity ($b = 0.272$, $p = 0.013$, 95%BootCIs [0.061, 0.447]) to the mediated path with indirect effects was significant when testosterone was added as a mediator ($b = 0.092$, $p = 0.005$, 95%BootCIs [0.026, 0.209]) (Fig. 3A).[2] The residual predictive power (direct effect) of family income on facial masculinity (c' path) did not remain significant ($b = 0.179$, $p = 0.134$, 95%BootCIs [−0.058, 0.373]) when the influence of testosterone on facial masculinity was partialled out. The percentage of variance accounted for by introducing testosterone as a mediator was 33.8% (VAF = indirect effect/total effect * 100 = 0.092/0.272 * 100 = 33.8%). Therefore, testosterone had a significant partial mediating effect between family income and facial masculinity.

3.3. Mediation analysis: family income, testosterone, adiposity, immune function

There were significant bivariate correlations between family income

[2] Unstandardized coefficients are shown in Fig. 3A and B: note that because it is not the amount of euros per month but family income category numbers (Table 1, numerical variable with a minimum of 1 and a maximum of 7) that were used in these analyses, a change of 1 in the model means that family income shifts to another income group, as described in Section 2.8.

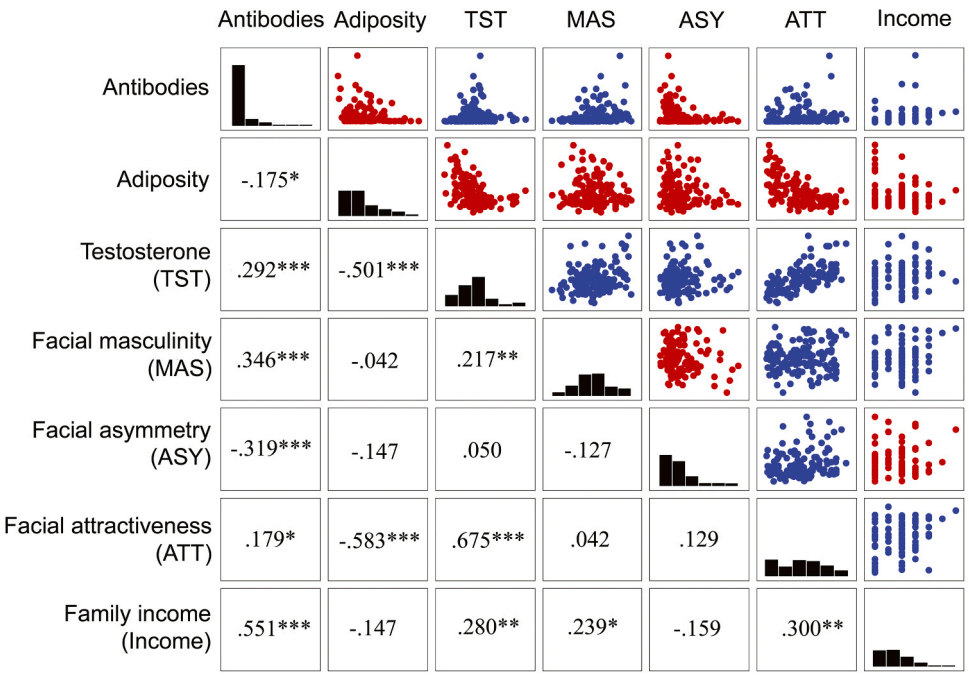

Fig. 2. Correlations between variables. Below the diagonal: Spearman correlation coefficients, with $*p < 0.05$; $**p < 0.01$; $***p < 0.001$. Above the diagonal: scatterplots showing the relationships between the variables, color-coded as blue (positive relationship) and red (negative relationship). Diagonal: distribution of data points for each variable. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

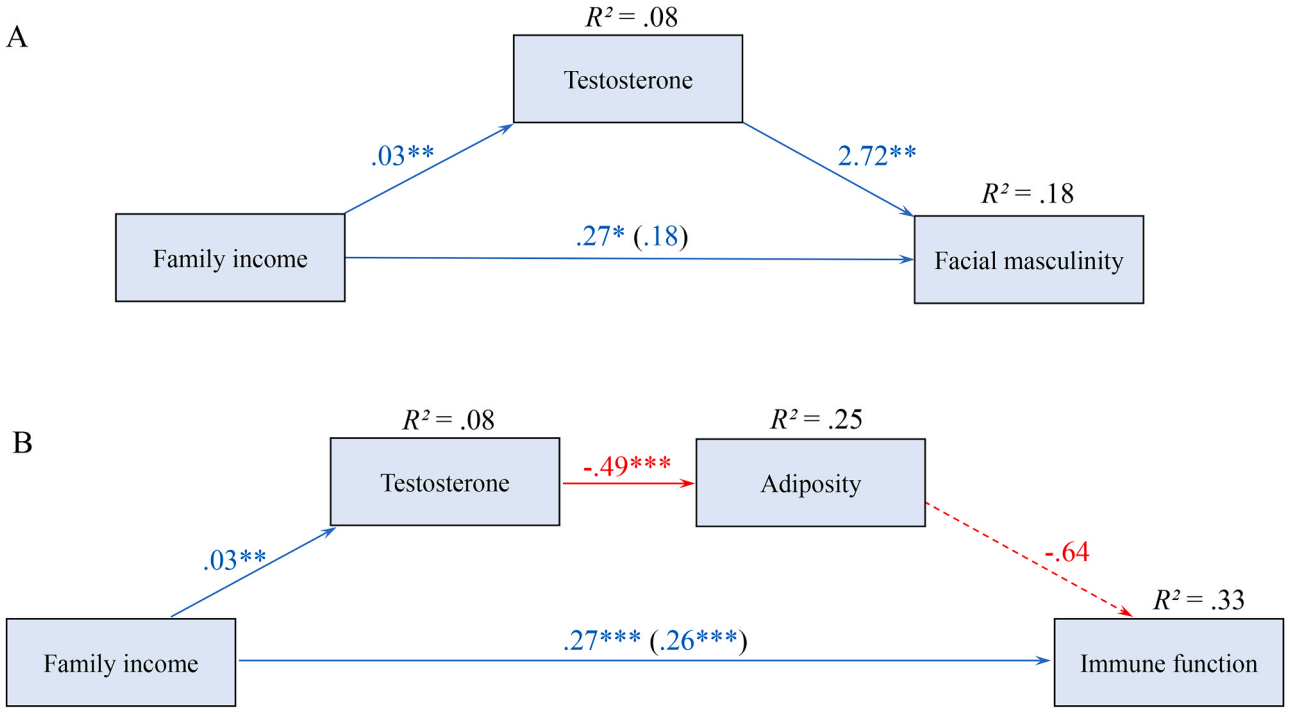

Fig. 3. (A) Mediation analysis linking family income to facial masculinity via testosterone. Unstandardized regression coefficients shown for each relationship, with $*p < 0.05$; $**p < 0.01$; $***p < 0.001$. Direct effect from family income to immune function (c' path) is shown in parentheses. Squared multiple correlations (R^2) are given for each endogenous variable. Positive relationships are shown in blue, negative ones in red. (B) Mediation analysis linking family income to immune response via testosterone and adiposity. Statistically non-significant relationships are shown with dashed arrows. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

and testosterone, testosterone and adiposity, adiposity and immune response, and family income and immune response (Fig. 2). To test prediction 7 about the mediating effects of testosterone and adiposity on immune function, we performed a mediation analysis with these variables entered into a SEM model. The change from the total effect (c path) of family income to antibody response ($b = 0.271$, $p < 0.001$, 95% BootCIs [0.178, 0.360]) to the mediated path with indirect effects was significant when testosterone and adiposity were added as mediators

($b = 0.011$, $p = 0.038$, 95%BootCIs [0.000, 0.039]) (Fig. 3B). The residual predictive power (direct effect) of family income on antibody response (c' path) remained significant ($b = 0.260$, $p < 0.001$, 95% BootCIs [0.164, 0.355]) when the influence of testosterone and adiposity on antibody response was partialled out. The percentage of variance accounted for by introducing testosterone and adiposity as mediators was 4% (VAF = indirect effect/total effect * 100 = 0.011/0.271 * 100 = 4%). This indicates that there are other important mechanisms besides testosterone and adiposity through which family income influences immune response, although testosterone and adiposity did have a significant partial mediating effect.

3.4. Multiple regression analysis: facial asymmetry, facial masculinity, adiposity, immune function

There were significant correlations between immune function and facial asymmetry ($r_s = -0.319$, $p < 0.001$, $n = 146$, Fig. 2) and between immune function and facial masculinity ($r_s = 0.346$, $p < 0.001$, $n = 146$; Fig. 2). The correlation between facial asymmetry and facial masculinity was weak and statistically non-significant ($r_s = -0.127$, $p = 0.127$, $n = 146$; Fig. 2), suggesting that these facial traits are mostly unrelated. We performed a linear multiple regression analysis to test prediction 8. The results showed that both facial asymmetry and facial masculinity remained significant predictors of immune function (Table 2). This multiple regression model with two predictors explained 16.9% of the variation in immune function ($R^2 = 0.169$). In a post-hoc test, we examined whether previous findings about facial adiposity being a better predictor of immune function than facial masculinity (Rantala et al., 2013) could be replicated in this sample using another measure of adiposity (i.e. body fat percentage). Adding adiposity as a third independent variable in the regression model showed that adiposity had statistically significant predictive power above and beyond facial masculinity and facial asymmetry (Table 3). The predictive power of this multiple regression model with three predictor variables was higher ($R^2 = 0.238$, $\Delta R^2 = 0.069$) than in the model with two predictor variables. These results indicate that higher facial masculinity, lower facial asymmetry, and lower adiposity (measured as body fat percentage) are reliable and independent cues of better immune function (Table 3).

3.5. Structural equation model

We constructed a structural equation model with all the variables used in this study to show the hypothesized causal relationships between the variables (Fig. 4). The model was based on our theoretical expectations. The model explained a relatively high proportion of variance in facial attractiveness (53%) and immune function (42%). The model explained a significant proportion of variance in adiposity (27%) but only limited variance in facial masculinity (16%), testosterone (12%), and facial asymmetry (9%). The model fit was considered good: $\chi 2$ (df = 8) = 12.304, $p = 0.138$, RMSEA = 0.061, CFI = 0.982).

4. Discussion

The main findings of this study are that men with higher family income during development had higher circulating testosterone, more robust immune function, higher facial masculinity, and higher facial attractiveness. Testosterone (positively) and adiposity (negatively) mediated the positive relationship between family income and immune function ($r_s = 0.551$). The effect of the mediation, however, was rather weak (VAF = 4%).[3] Testosterone partially (VAF = 38.7%) mediated the effect of family income on facial masculinity, as predicted, although we measured testosterone only in early adulthood and not longitudinally. We interpret this result in such a way that current testosterone levels serve as a proxy of testosterone levels in ontogeny, which would have had a more direct causal role on the development of facial masculinity. The only predictions that were not fully borne out by the data concerned the relationship between family income and adiposity, and family income and facial asymmetry. The relationships between these variables were in the predicted direction (Fig. 2), but our study sample was not adequately powered to provide statistically significant support for such weak associations as were found in the data for these relationships.

We also found that higher facial symmetry, higher facial masculinity, and lower adiposity (body fat percentage) were valid and independent cues of a more robust immune response. Phalane et al. (2017) found that African men with masculine faces had high cytokine response while more symmetrical men had weaker cytokine response. Importantly, both types of men's faces were considered healthy and attractive by women raters. We did not fully replicate Phalane et al.'s (2017) findings in our sample of Latvian men, as men with more symmetrical faces had a more robust immune response. The direct negative effect of immune function on facial asymmetry (Fig. 4) suggests that the development of these traits is interlinked and that higher facial asymmetry can serve as a biomarker of less robust immune function. Although many previous studies demonstrated negative relationships between the condition of the environment or genetic quality of the organisms and the asymmetry of facial and bodily parameters (Fink et al., 2006), a number of studies found no significant association between costly morphological traits and environmental stress (Graham and Özener, 2016). The results of this study show that the interplay between costly phenotypic traits (such as immune function and facial attractiveness) and environmental stress may be more dynamic and complex because the optimal functioning of the immune system may be based on the availability of resources in the environment where the organism develops.

The fact that we found strong correlations between facial attractiveness, adiposity, and testosterone—but only weak correlations between facial attractiveness, facial masculinity, and fluctuating asymmetry (Fig. 2)—is consistent with the idea that variation in testosterone levels tracks fluctuations in health status (Muehlenbein and Bribiescas, 2005). As there is a bidirectional relationship between testosterone and adiposity (Kelly and Jones, 2015; Rantala et al., 2013), and as health is positively associated with attractiveness and attractiveness is negatively associated with adiposity (Stephen and Luoto, 2021; Sugiyama, 2015), it is logical that variation in health status should

Table 2
A multiple regression model with two predictor variables and immune function as an outcome variable ($N = 146$). Data on facial asymmetry and immune function were transformed (as described in *Method*).

Variable	Estimate	Std. error	t	p	VIF
(Intercept)	1.27	0.339	3.751	<0.001***	
Facial masculinity	0.193	0.049	3.951	<0.001***	1.014
Facial asymmetry	-0.764	0.239	-3.199	0.002**	1.014

** $p < 0.01$.
*** $p < 0.001$.

Table 3
A multiple regression model with three predictor variables and immune function as an outcome variable ($N = 146$). Data on facial asymmetry, adiposity, and immune function were transformed (as described in *Method*).

Variable	Estimate	Std. error	t	p	VIF
(Intercept)	2.884	0.555	5.193	<0.001***	
Facial masculinity	0.18	0.047	3.829	<0.001***	1.019
Facial asymmetry	-0.894	0.232	-3.849	<0.001***	1.039
Adiposity	-1.277	0.356	-3.585	<0.001***	1.028

*** $p < 0.001$.

[3] For the proportion of variance accounted for (VAF) in one variable by another, small, medium, and large effect sizes are defined as 0.01, 0.09, and 0.25 (Preacher and Kelley, 2011).

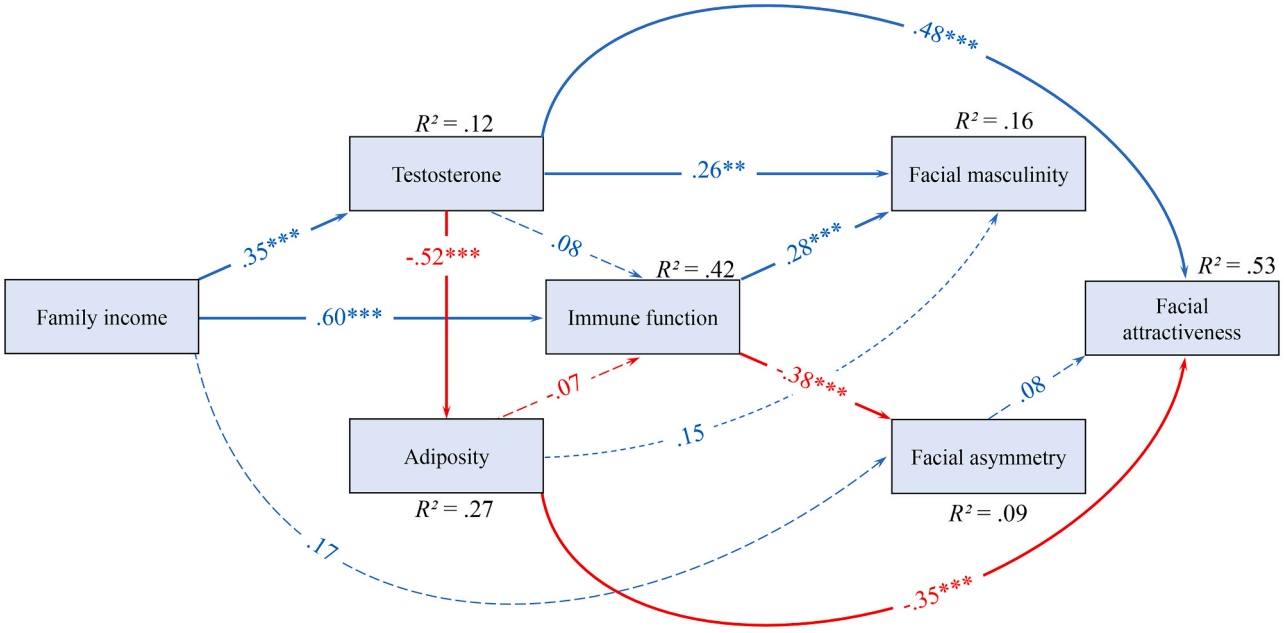

Fig. 4. Structural equation model showing causal links between all measured variables. Standardized regression coefficients shown for each relationship, with $^{*}p < 0.05$; $^{**}p < 0.01$; $^{***}p < 0.001$. Statistically significant relationships are shown with bolded arrows; non-significant relationships are shown with dashed arrows. Squared multiple correlations (R^2) are given for each endogenous variable. Positive relationships are shown in blue, negative ones in red. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

be linked with attractiveness partially via testosterone and adiposity. However, the associations between facial attractiveness, facial masculinity, and facial asymmetry were non-existent or weak (Fig. 2), potentially because facial masculinity and asymmetry are proxies of developmental rather than current conditions, and it is more logical for attractiveness ratings to be associated with current rather than developmental conditions. It is also possible that the null finding between facial masculinity and attractiveness arose because of the relatively poor socioeconomic conditions of the study sample. Cross-national research has, after all, shown that women's preferences for facial masculinity are stronger under conditions in which offspring survival is higher and economic conditions are more favorable (Marcinkowska et al., 2019).

This study was limited in that only one facet of immune function was used (i.e. the ability to produce an immune response against a novel antigen). While using a phenotypic over a genotypic measure (e.g., Zaidi et al., 2019) of immune function has clear advantages because of the resource-dependent nature of immune development (Krams et al., 2019; Rubika et al., 2020), studies that utilize a range of different measures of immune function will naturally provide the most holistic information about immunity and its different facets (Foo et al., 2020). Whereas prior research has suggested that facial masculinity (Zaidi et al., 2019) and facial symmetry (Phalane et al., 2017) do not reflect robustness of immune function as measured by MHC heterozygosity (Zaidi et al., 2019) and cytokine levels (Phalane et al., 2017), our results indicate that facial asymmetry may in fact be as reliable an indicator of immune function as facial masculinity, and that these indicators are non-overlapping. The predictive power of facial masculinity and facial asymmetry may depend on how immune function is measured, however, as other research using functional cytokine analysis of Peripheral Blood Mononuclear Cells (PBMCs) after Lipopolysaccharide (LPS) stimulation has found that masculinity rather than symmetry is a more reliable cue of immune function (Phalane et al., 2017).

Although the current study design was insufficient for distinguishing between environmental and genetic factors affecting human development (White and Puts, 2019), other studies support our findings that the environment plays a significant role in inducing and guiding individual development, including immune function and fluctuating asymmetry (Beasley et al., 2013; Frankenhuis et al., 2019; Krams et al., 2019 Luoto et al., 2019b). The complex interplay between genes, environment, and phenotypic plasticity can even give rise to distinctive phenotypes such as color morphs (Gilbert, 2005), diet morphs (Levis et al., 2018), or high variation in traits such as adiposity (Maner et al., 2017; Rantala et al., 2019) and antibody levels, as found in this study. This makes childhood conditions in general and family income in particular highly important parameters to be included in human eco-immunological research (Bourke et al., 2016; DeBoer et al., 2017; Krams et al., 2019), especially under conditions of resource scarcity and/or in conditions of high income inequality. Our results further highlight the role of fluctuating asymmetry in immunological research since it has been associated with such medical parameters as susceptibility to infections (Van Dongen and Gangestad, 2011) and indicators of stress and mental health (Borráz-León et al., 2019; Borráz-León et al., In preparation). We expect future studies to seek closer integration between resource availability, developmental conditions, immune function, fluctuating asymmetry, and other physiological and health parameters, particularly in the context of sexual selection and/or evolutionary life history theory.

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CRediT authorship contribution statement

IAK, **MJR**, **TK**, and **IS:** Conceptualization. **IAK**, **MJR**, **IS**, **TK**, **SL**, **FRM**, and **JC-G:** Methodology. **GT**, **SL**, **DE**, **IAK**, **JIB-L**, **EB**, and **AR:** Formal analyses. **IAK**, **IS**, **MJR**, and **RK:** Collected data. **AR**, **SL**, and **IAK:** Writing - original draft. **SL**, **AR**, **IAK**, **FRM**, **TK**, **RK**, **JIB-L**, **MJR**, and **JG-C**: Writing - review & editing. **SL**, **GT**, and **DE**: Designed figures. **MJR**, **IAK**, and **TK**: Funding acquisition, Supervision, and administration of the project.

Declaration of Competing Interest

The authors declare no competing interests.

Data availability

All data are available in the main text or supplemental materials.

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References

Adam, E.K., Quinn, M.E., Tavernier, R., McQuillan, M.T., Dahlke, K.A., Gilbert, K.E., 2017. Diurnal cortisol slopes and mental and physical health outcomes: a systematic review and meta-analysis. Psychoneuroendocrinology 83, 25–41.

Beasley, D.A.E., Bonisoli-Alquati, A., Mousseau, T.A., 2013. The use of fluctuating asymmetry as a measure of environmentally induced developmental instability: a meta-analysis. Ecol. Indic. 30, 218–226.

Blanckenhorn, W.U., Hosken, D.J., 2003. The heritability of three condition measures in the yellow dung fly. Behav. Ecol. 14, 612–618.

Borráz-León, J.I., Cerda-Molina, A.L., Mayagoitia-Novales, L., 2017a. Testosterone level changes after perceiving the body odour of a posible rival in human males: the role of facial symmetry. Behaviour 154, 677–691.

Borráz-León, J.I., Cerda-Molina, A.L., Mayagoitia-Novales, L., 2017b. Stress and cortisol responses in men: differences according to facial symmetry. Stress 20, 573–579.

Borráz-León, J.I., Cerda-Molina, A.L., Rantala, M.J., Mayagoitia-Novales, L., 2018. Choosing fighting competitors among men: testosterone, personality, and motivations. Evol. Psychol. 16, 147470491875724, 1474704918757243.

Borráz-León, J.I., Rantala, M.J., Cerda-Molina, A.L., 2019. Digit ratio (2D:4D) and facial fluctuating asymmetry as predictors of the dark triad of personality. Personal. Individ. Differ. 137, 50–55.

Borráz-León, J.I., Rantala, M.J., Luoto, S., Krams, I., Contreras-Garduño, J., Cerda-Molina, A.L., Krama, T., 2021. Toxoplasma gondii and psychopathology: latent infection is associated with interpersonal sensitivity, psychoticism, and higher testosterone levels in men, but not in women. Adapt. Hum. Behav. Physiol. 1–15.

J.I. Borráz-León, M.J. Rantala, S. Luoto, I. Krams, J. Contreras-Garduño, T. Krama, A.L. Cerda-Molina, In preparation. Self-perceived facial attractiveness, fluctuating asymmetry, and minor ailments predict mental health outcomes. Int. J. Environ. Res. Public Health.

Bourke, C.D., Berkley, J.A., Prendergast, A.J., 2016. Immune dysfunction as a cause and consequence of malnutrition. Trends Immunol. 37, P386–P398.

Brownlee, K.K., Moore, A.W., Hackney, A.C., 2005. Relationship between circulating cortisol and testosterone: influence of physical exercise. J. Sports Sci. Med. 4, 76–83.

Central Statistics Office of Latvia, 2020. [Online database]. https://www.csb.gov.lv/en/sakums. Accessed 20 December 2020.

DeBoer, M.D., Scharf, R.J., Leite, A.M., Ferrer, A., Havt, A., Pinkerton, R., Lima, A.A., Guerrant, R.L., 2017. Systemic inflammation, growth factors, and linear growth in the setting of infection and malnutrition. Nutrition 33, 248–253.

Delves, P.J., Roitt, I.M., 2000. The immune system. N. Engl. J. Med. 343, 37–49.

Dunson, D.B., Baird, D.D., Wilcox, A.J., Weinberg, C.R., 1999. Day-specific probabilities of clinical pregnancy based on two studies with imperfect measures of ovulation. Hum. Reprod. 14, 1835–1839. https://doi.org/10.1093/humrep/14.7.1835.

Ekrami, O., Claes, P., Shriver, M.D., Weinberg, S.M., Marazita, M.L., Walsh, S., Van Dongen, S., 2021. Effects of male facial masculinity on perceived attractiveness. Adapt. Hum. Behav. Physiol. 7, 73–88.

Ellis, B.J., Del Giudice, M., 2019. Developmental adaptation to stress: an evolutionary perspective. Ann. Rev. Psychol. 70, 111–139.

Fink, B., Neave, N., Manning, J.T., Grammer, K., 2006. Facial symmetry and judgements of attractiveness, health and personality. Personal. Individ. Differ. 41, 491–499.

Folstad, I., Karter, A.J., 1992. Parasites, bright males, and the immunocompetence handicap. Am. Nat. 139, 603–622 doi:org/10.1086/285346.

Foo, Y.Z., Nakagawa, S., Rhodes, G., Simmons, L.W., 2017. The effects of sex hormones on immune function: a meta-analysis. Biol. Rev. 92, 551–571 doi:org/10.1111/brv.12243.

Foo, Y.Z., Simmons, L.W., Perrett, D.I., Holt, P.G., Eastwood, P.R., Rhodes, G., 2020. Immune function during early adolescence positively predicts adult facial sexual dimorphism in both men and women. Evol. Hum. Behav. 41, 199–209.

Francisco, V., Pino, J., Campos-Cabaleiro, V., Ruiz-Fernández, C., Mera, A., Gonzalez-Gay, M.A., Gomez, R., Gualillo, O., 2018. Obesity, fat mass and immune system: role for leptin. Front. Physiol. 9, 640.

Frankenhuis, W.E., Nettle, D., Dall, S.R., 2019. A case for environmental statistics of early-life effects. Phil. Trans. R. Soc. B 374, 20180110.

Gangestad, S.W., Thornhill, R., Yeo, R.A., 1994. Facial attractiveness, developmental stability, and fluctuating asymmetry. Ethol. Sociobiol. 15, 73–85.

Gangestad, S.W., Merriman, L.A., Thompson, M.E., 2010. Men's oxidative stress, fluctuating asymmetry and physical attractiveness. Anim. Behav. 80, 1005–1013.

Gilbert, S.F., 2005. Mechanisms for the environmental regulation of gene expression: ecological aspects of animal development. J. Biosci. 30, 65–74.

Graham, J.H., Özener, B., 2016. Fluctuating asymmetry of human populations: a review. Symmetry 8, 154. https://doi.org/10.3390/sym8120154.

Gupta, T., Santos, C.S.A., Sotillo, A., De Neve, L., Stienen, E.W.M., Müller, W., Lens, L., 2016. Nutritional stress causes heterogeneous relationships with multi-trait FA in lesser black-backed gull chicks: an aviary experiment. Symmetry 8, 133. https://doi.org/10.3390/sym8110133.

Hughes, A., Kumari, M., 2019. Testosterone, risk, and socioeconomic position in British men: exploring causal directionality. Soc. Sci. Med. 220, 129–140.

Kelly, D.M., Jones, T.H., 2015. Testosterone and obesity. Obes. Rev. 16, 581–606.

Krams, I., Vrublevska, J., Cirule, D., Kivleniece, I., Krama, T., Rantala, M.J., Sild, E., Hõrak, P., 2012. Heterophil/lymphocyte ratios predict the magnitude of humoral immune response to a novel antigen in great tits (Parus major). Comp. Biochem. Physiol Part A Mol. Integr. Physiol. 161, 422–428.

Krams, I., Vrublevska, J., Cīrule, D., Kivleniece, I., Krama, T., Rantala, M.J., Kaasik, A., Hõrak, P., Sepp, T., 2013. Stress, behaviour and immunity in wild-caught wintering great tits (Parus major). Ethology 119, 397–406.

Krams, I., Luoto, S., Rubika, A., Krama, T., Elferts, D., Kecko, S., Skrinda, I., Moore, F.R., Krams, R., Rantala, M.J., 2019. A head start for life history development? Family income causes associations between body height and immune response in men. Am. J. Phys. Anthropol. 168, 421–427 doi:org/10.1002/ajpa.23754.

Krams, I.A., Skrinda, I., Kecko, S., Moore, F.R., Krama, T., Kaasik, A., Meija, L., Lietuvietis, V., Rantala, M.J., 2014. Body height affects the strength of immune response in young men, but not young women. Sci. Rep. 4, 6223.

Lauringson, V., Veldre, G., Hõrak, P., 2020. Adolescent cranial volume as a sensitive marker of parental investment: the role of non-material resources? Front. Psychol. 11, 3624.

Levis, N.A., Isdaner, A.J., Pfennig, D.W., 2018. Morphological novelty emerges from pre-existing phenotypic plasticity. Nat. Ecol. Evol. 2, 1289–1297.

Luoto, S., 2019. An updated theoretical framework for human sexual selection: from ecology, genetics, and life history to extended phenotypes. Adapt. Hum. Behav. Physiol. 51, 48–102 doi:org/10.1007/s40750-018-0103-6.

Luoto, S., Krams, I., Rantala, M.J., 2019a. A life history approach to the female sexual orientation spectrum: evolution, development, causal mechanisms, and health. Arch. Sex. Behav. 48, 1273–1308 doi:org/10.1007/s10508-018-1261-0.

Luoto, S., Krams, I., Rantala, M.J., 2019b. Response to commentaries: life history evolution, causal mechanisms, and female sexual orientation. Arch. Sex. Behav. 48, 1335–1347 doi:org/10.1007/s10508-019-1439-0.

Maner, J.K., Dittmann, A., Meltzer, A.L., McNulty, J.K., 2017. Implications of life-history strategies for obesity. Proc. Natl. Acad. Sci. 114, 8517–8522.

Marcinkowska, U.M., Rantala, M.J., Lee, A.J., Kozlov, M.V., Aavik, T., Cai, H., Contreras-Garduño, J., David, O.A., Kaminski, G., Li, N.P., Onyishi, I.E., Prasai, K., Pazhoohi, F., Prokop, P., Rosales Cardozo, S.L., Sydney, N., Taniguchi, H., Krams, I., Dixson, B.J.W., 2019. Women's preferences for men's facial masculinity are strongest under favorable ecological conditions. Sci. Rep. 9, 3387.

Muehlenbein, M.P., Bribiescas, R.G., 2005. Testosterone-mediated immune functions and male life histories. Am. J. Hum. Biol. 17, 527–558.

Phalane, K.G., Tribe, C., Steel, H.C., Cholo, M.C., Coetzee, V., 2017. Facial appearance reveals immunity in African men. Sci. Rep. 7, 7443.

Preacher, K.J., Kelley, K., 2011. Effect size measures for mediation models: quantitative strategies for communicating indirect effects. Psychol. Methods 16, 93–115.

Prendergast, A.J., Humphrey, J.H., 2014. The stunting syndrome in developing countries. Paediatr. Int. Child Health 34, 250–265.

Rantala, M.J., Moore, F.R., Skrinda, I., Krama, T., Kivleniece, I., Kecko, S., Krams, I., 2012. Evidence for the stress-linked immunocompetence handicap hypothesis in humans. Nat. Commun. 3, 694. https://doi.org/10.1038/ncomms1696.

Rantala, M.J., Coetzee, V., Moore, F.R., Skrinda, I., Kecko, S., Krama, T., Kivleniece, I., Krams, I., 2013. Adiposity, compared with masculinity, serves as a more valid cue to immunocompetence in human mate choice. Proc. R. Soc. B B 280, 20122495. https://doi.org/10.1098/rspb.2012.2495.

Rantala, M.J., Luoto, S., Krams, I., 2019. Eating disorders: an evolutionary psychoneuroimmunological approach. Front. Psychol. 10, 2200.

Roved, J., Westerdahl, H., Hasselquist, D., 2017. Sex differences in immune responses: hormonal effects, antagonistic selection, and evolutionary consequences. Horm. Behav. 88, 95–105.

Rubika, A., Luoto, S., Krama, T., Trakimas, G., Rantala, M.J., Moore, F.R., Skrinda, I., Elferts, D., Krams, R., Contreras-Garduño, J., Krams, I.A., 2020. Women's socioeconomic position in ontogeny is associated with improved immune function and lower stress, but not with height. Sci. Rep. 10, 11517.

Schönberger, K., Riedel, C., Rückinger, S., Mansmann, U., Jilg, W., Kries, R.V., 2013. Determinants of long-term protection after hepatitis B vaccination in infancy: a meta-analysis. Pediatr. Infect. Dis. J. 32, 307–313.

Skrinda, I., Krama, T., Kecko, S., Moore, F.R., Kaasik, A., Meija, L., Lietuvietis, V., Rantala, M.J., Krams, I., 2014. Body height, immunity, facial and vocal attractiveness in young men. Naturwissenschaften 101, 1017–1025.

Sohda, S., Suzuki, K., Igari, I., 2017. Relationship between the menstrual cycle and timing of ovulation revealed by new protocols: analysis of data from a self-tracking health app. J. Med. Internet Res. 19, e391.

Stephen, I., Luoto, S., 2021. Physical cues of partner quality. In: Mogilski, J., Shackelford, T. (Eds.), The Oxford Handbook of Evolutionary Psychology and Romantic Relationships. Oxford University Press, Oxford. https://doi.org/10.31234/osf.io/pk84y.

Sugiyama, L.S., 2015. Physical attractiveness: an adaptationist perspective. In: Buss, D. M. (Ed.), The Handbook of Evolutionary Psychology, second ed. Wiley Online Library, pp. 317–384. https://doi.org/10.1002/9781119125563.evpsych112.

Tyrrell, J., Jones, S.E., Beaumont, R., Astley, C.M., Lovell, R., Yaghootkar, H., Tuke, M., Ruth, K.S., Freathy, R.M., Hirschhorn, J.N., Wood, A.R., Murray, A., Weedon, M.N., Frayling, T.M., 2016. Height, body mass index, and socioeconomic status: mendelian randomisation study in UK Biobank. BMJ 352, i582. https://doi.org/10.1136/bmj.i582.

United Nations, United Nations Statistics Division - Demographic and Social Statistics, 2020. [Online database]. Unstats.un.org. (Accessed 20 December 2020).

Van Dongen, S., Gangestad, S.W., 2011. Human fluctuating asymmetry in relation to health and quality: a meta-analysis. Evol. Hum. Behav. 32, 380–398.

White, J.D., Puts, D.A., 2019. Genes influence facial attractiveness through intricate biological relationships. PLOS Genetics 15, e1008030.

Zaidi, A.A., White, J.D., Mattern, B.C., Liebowitz, C.R., Puts, D.A., Claes, P., Shriver, M. D., 2019. Facial masculinity does not appear to be a condition-dependent male ornament and does not reflect MHC heterozygosity in humans. Proc. Natl. Acad. Sci. 116, 1633–1638.

Zietsch, B.P., Lee, A.J., Sherlock, J.M., Jern, P., 2015. Variation in women's preferences regarding male facial masculinity is better explained by genetic differences than by previously identified context-dependent effects. Psychol. Sci. 26, 1440–1448.