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# A head start for life history development? Family income mediates associations between height and immune response in men

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# A head start for life history development? Family income mediates associations between height and immune response in men

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**KEYWORDS:** immunity, nutrition, socioeconomic status, stature, life history theory

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## ABSTRACT

**Objectives.** Male height and health affect a diverse range of social and economic outcomes such as competition for resources and mates. Life history theory predicts that limited availability of bioenergetic resources curbs the development of central life history functions such as somatic growth, immunity and investment in offspring. Although genetic factors are important determinants of height, other factors such as income level may affect the incidence of infections during ontogeny, thus having indirect effects on somatic growth. We tested whether growing up in families with a higher income positively affects height and immune function.

**Materials and Methods.** Seventy-three young Latvian men from various socioeconomic backgrounds were given a hepatitis B vaccine. Blood samples were subsequently collected to measure the antibodies produced in response to the vaccination. Tweedie compound Poisson generalized linear models were used to examine relationships between height, family income and antibody titers.

**Results.** Both height and family income positively correlated with the strength of men's immune response. However, when testing for the simultaneous effects of height and income on antibody titers, the statistical models showed that height affected antibody levels indirectly because income level mediated variance in height.

**Discussion.** The results of this study show that the relationships between height and immune function in young men are more complex than previously thought. Associations between taller stature of men and the robustness of their immune response are indirect because resource availability affects both somatic growth and the development of the immune system.


## 1 | INTRODUCTION

Life history theory posits that the principal functions of self-management and reproduction need adequate resource allocations that are extracted from the finite amounts of energy that every organism has at its disposal (Ellison, 2017; Said-Mohamed, Pettifor, & Norris, 2018). This creates a natural constraint on the organism's adaptations and limits its fitness potential (Stearns, 1992). Although secondary sexual characters are not directly a part of the reproductive system of an organism, they are the product of sexual selection, giving fitness-related advantages over the organism's rivals (Cornwallis & Uller, 2010; Polo et al., 2018). It has been suggested that secondary sexual traits such as large body size reliably signal the condition of a male by acting as a bioenergetic handicap (Folstad & Karter, 1992; Zahavi, 1975). Development and maintenance of such traits are often energetically costly, and individuals are typically limited in their capacity to make optimal energy allocations to each competing demand (Said-Mohamed et al., 2018; Stearns, 1989).

Body size in human males is an important biological trait which affects a diverse range of outcomes such as attractiveness to potential mates and competition for resources (Patel & Devaraj, 2017; Pawłowski, Dunbar, & Lipowicz, 2000; Polo et al., 2018; Sell et al., 2017; Stulp & Barrett, 2016). In ontogeny, somatic growth and development of the immune system are thought to compete for the same resources, potentially impairing growth (Pawłowski, Nowak, Borkowska, Augustyniak, & Drulis-Kawa, 2017; Stearns, 1992). However, taller stature will bring considerable socioeconomic and biological benefits in males during adulthood. For example, in developed countries, taller stature of males is associated with higher socioeconomic status, higher status rank with regard to employment and better reproductive success (Case & Paxson, 2008; Grabner, 2012; Lundborg, Nystedt, & Rooth, 2014; Pawłowski et al., 2000; Stulp, Buunk, Verhulst, & Pollet, 2015; Tyrell et al., 2016).

Height is sensitive to infection frequency during childhood (Hwang et al., 2013; Joel et al., 2014; Kopacova et al., 2014), which suggests that taller men have better health in general and enhanced immune function in particular. Although our previous analyses of the current data set have shown that height is positively correlated with the strength of immune response to hepatitis B vaccination in males (Krams et al., 2014; Skrinda et al., 2014), other studies did not find direct relationships between height and the strength of immune response against a novel antigen in males (Averhoff et al., 1998; Lord, 2013; Pawłowski et al., 2017). However, a vaccination study done in Poland (Pawłowski et al., 2017) found a near-significant relationship ($P$ = 0.06) between height and innate immunity response measured by total complement activity.

Findings on the potential causes and consequences of adult height indicate that stature can be used as a measure of cumulative net nutrition (Perkins et al., 2016). Perkins and colleagues (2016) show that lower stature reflects growth retardation in low- and middle-income countries and is driven mostly by environmental conditions such as net nutrition during early years of development. They suggest that adult height is a marker of variation in cumulative net nutrition and standard of living between and within populations, countries and economies. It is important to note that the influence of malnutrition on resistance to infection is well established since it is the primary cause of immunodeficiency (Bourke, Berkley, & Prendergast, 2016) and slower growth (DeBoer et al., 2017).

The critical window for developmental plasticity of body growth and immunity occurs when mothers buffer infants against environmental threats and when the infant's growth is most sensitive to maternal nutrition (McDade, 2003; Georgiev, Kuzawa, & McDade, 2016; Said-Mohamed et al., 2018). In wealthier Western societies, approximately 80% of between-population variation in height is determined by genetic factors, while environmental factors such as pathogens, infections and the level of income play a less important role in heritability (McEvoy & Visscher, 2009; Silventoinen et al., 2003). However, in poorer Western countries, such as Latvia, economic factors may be of crucial importance. In these countries, central and local governments often cannot cover basic social needs, which could affect the quality of life and have an impact on environmental factors that influence child health and growth (Joel et al., 2014; Kopacova et al., 2014; Sekiyama, Roosita, & Ohtsuka, 2018). For example, lower socioeconomic status, income and education have been associated with higher cardiovascular risk (Jenkins & Ofstedal, 2014; Winkleby et al., 1992) and mental health problems (Goldman et al., 2018). Adult height is thus an important longitudinal marker for tracking cumulative net nutrition and population health (Perkins, Subramanian, Davey Smith, & Özaltin, 2016; Sekiyama et al., 2018).

In this study, we reanalyzed a part of the data sets used in Krams et al. (2014) and Skrinda et al. (2014) and used additional data that have not been analyzed before. We tested whether young men with higher stature and better immunity grew up in families with a higher income.

## 2 | MATERIALS AND METHODS

### 2.1 | Participants and height

We studied associations among height, antibody titers against hepatitis B antigen and socioeconomic status of seventy-three young Latvian men (20.84 ± 0.65 years old, mean ± SD, range 19-22 years) in southeastern Latvia in 2010. Participants were students from Daugavpils University and Transportation College of Daugavpils. We measured height of participants between 8.00 and 11.00 A.M. with a precision of 0.5 cm using a Seca 222 measuring rod (Seca, Hamburg, Germany) as described elsewhere (Krams et al., 2014; Skrinda et al., 2014). The average height for the current sample was 181.49 ± 10.54 cm, while the average height for 20-21-year-old men is 181.04 ± 10.82 cm in our study population (Skrinda et al., 2014).

During a series of studies we obtained a sample containing data on more than 150 young men. This study included only those participants 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 any serious diseases). None of the participants was dropped from this analysis due to serious disease, smoking or drugs. Finally, none of the participants was overweight or obese: their body mass index fell within the normal body mass index range (< 25).

### 2.2 | Immune system assay

Hepatitis B is a serious viral infection that can cause both acute and chronic liver disease. Approximately 257 million people are living with hepatitis B virus infection (defined as hepatitis B surface antigen positive). This infection is transmitted through contact with the blood or other body fluids of an infected person. Hepatitis B can be prevented by safe and effective vaccines (Zuin et al., 1992). 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. 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-HBsAg 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-HBsAg.

### 2.3 | Socioeconomic status

There are several important variables that characterize the socioeconomic status of an individual. It is crucial to know the following parameters: age, education, job class and income (often represented as annual household income of the individual: e.g., Tyrrell et al., 2016). The participants were 19-22-year-old men; all were undergraduate students with no job class achieved and without any opportunity to work (none worked either before or during the study) because of their full-time studies. The participants all lived with their parents during the study. Thus, all socioeconomic parameters except family income 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 current statistical analyses were done based on the total family income divided by the number of family members. We included in the study only those families 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 (e.g., Lavrinoviča, Lavriņenko, & Teivāns-Treinovskis, 2012).

In 2000, Latvia's population was 2.38 million people (United Nations, 2017); in 2018, it was 1.93 million (Central Statistics Office of Latvia, 2018). No other country has had a more precipitous fall in population during that period (United Nations, 2017). 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. The average monthly wage in this region is about half of the average wage in Latvia (Central Statistics Office of Latvia, 2018). These factors created an environment where few study participants were able to improve their family income across decades.

The final data set did not include six participants who shifted away from their original socioeconomic status by more than one income category and five participants who regularly visited the United Kingdom, which positively affected their family income.

## 2.4 | Statistics

Antibody level data were not normally distributed because of an excessive number of zero values. The data did not reach normality after logarithmic transformation. Therefore, the Tweedie compound Poisson generalized linear models (cpglm) as implemented in R 3.4.3 (R Core Team 2017) library cplm (Zhang, 2013) were used to determine the relationship between the independent variables (height and income per family member / month$^{-1}$) and antibody titers. Bootstrap method with 2000 replicates were used to calculate confidence intervals for the model's predicted values. Spearman correlation analysis was used to test relationships between variables.

## 2.5 | Ethics statement

The study was approved by the Research Ethics Committee of the University of Daugavpils, 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.

## 3 | RESULTS

Nineteen out of 73 (26 %) young men failed to develop seroprotection against hepatitis B virus and none of them developed ≥10 mIU $ml^{-1}$ of anti-HBsAg. Height of young men significantly and positively correlated with antibody titers one month after the vaccination ($r_s = 0.369$, $P = 0.001$; Fig. 1). [Figure 1 here] We also found a positive correlation between family income and antibody titers ($r_s = 0.649$, $P < 001$; Fig. 2), and income and height ($r_s = 0.501$, $P < 0.001$; Fig. 3). [Figure 2 here] [Figure 3 here] However, a model that tested simultaneous effects of income and height on antibody titers revealed a significant effect caused only by income (Table 1), while the effect of height was non-significant (Table 1). This shows that stature affected antibody titers indirectly and income level mediated this effect, suggesting a significant role of resource availability on immune function and body growth in young men.

[Table 1 here]

## 4 | DISCUSSION

Overall, our results suggest that the development of bioenergetically expensive traits is limited by resource availability. We found that income per family member affects both height and the strength of immune response as shown by our correlation analyses. However, the Tweedie compound Poisson generalized linear model revealed a more complex effect of income level and height on the antibody response. The model showed a significant effect of income on antibodies while height was not a significant predictor of the strength of immune response. The model did not confirm the non-linear relationships between height and the immune function shown in Krams et al. (2014) and Skrinda et al. (2014).

Overall, while our results suggest a positive link between height and antibody response, the results also show that height affects immune function only by being associated with income. This is an important finding because it suggests that the relationship between height and immunity is driven by resource availability during ontogeny. This finding also suggests that sexual selection on physical traits in humans (Pawłowski et al., 2000; Polo et al., 2018; Stulp & Barrett, 2016) may be mediated by income because resource availability can increase the sexual attractiveness of men by making them taller. The finding has additional implications for research methodologies on natural variation in height and immune function under changing ecological/economic conditions. In particular, future studies on the relationship between height, body condition, genetic factors and immunity should take into account the socioeconomic aspects of environment during ontogeny (Perkins et al., 2016), partly because these aspects may have the potential to cause epigenetic effects and profoundly shape the developmental niche (Jablonka, 2017; Jablonka & Lamb, 2005; Stotz, 2017).

Height is considered to be one of the most heritable human traits (Lettre, 2011). However, cross-population differences suggest a number of environmental factors responsible for height variations (Bogin, 2013; Cole, 2000; Tanner, 1992). Resource availability, childhood and adolescent nutrition, and social, economic and political aspects are listed as the most important determinants of the environment that predict growth (Bogin, 2013; Cole 2000; NCD Risk Factor Collaboration, 2016; Perkins et al. 2016). Nevertheless, our study design cannot rule out genetic factors as contributing to the observed results. Although variation in the human immune system seems largely driven by environmental factors (Brodin et al., 2015), it is possible that some of the covariation that we found between height, immune response and family income is driven by genetic rather than environmental factors. Likewise, although existing evidence reviewed above highlights the importance of resource availability in early development to immune function and height, we cannot rule out *current* income as a potential factor influencing our results.

Besides affecting height, genetic differences may also contribute to variation in childhood socioeconomic conditions (Hill et al., 2016; Sherlock & Zietsch, 2017 and references therein; cf. Hill et al., 2018a,b; Okbay et al., 2016). Postulated proximate mechanisms underlying genetic influences on socioeconomic status include present orientation, impulsivity, educational attainment and life history strategies (Hampton, Asadi, & Olson 2018; Lee et al., 2018; Minkov & Bond, 2015; Minkov, Welzel, & Bond, 2016; Pepper & Nettle, 2017).

More generally, it is therefore possible that our results reflect the existence of coadapted life history strategies, where traits that promote future orientation and organismal longevity cluster together in meaningful functional composites (Figueredo, Vasquez, Brumbach, & Schneider, 2004; Figueredo et al., 2005; Minkov & Bond, 2015; Luoto, Krams, & Rantala, 2018; Sherlock & Zietsch, 2017). The link between family income and height suggests one such composite, indicating the existence of slower life history strategies in families with higher income (cf. Cabeza de Baca et al., 2016; Griskevicius et al., 2011; Lynch, 2016; Woodley of Menie et al., 2017). Our results are generally consistent with the hypothesis that internal factors (here: less robust immunity system) that increase susceptibility to infectious disease affect differences in life history strategies at the phenotypic (Murray, Gildersleeve, Fales, & Haselton, 2017) and genotypic levels (Figueredo et al., 2004). Women with less robust immunity systems, for instance, were reported to have faster life history strategies measured via sexual behaviors and attitudes (Murray, Gildersleeve, Fales, & Haselton, 2017). Broader life history conclusions on our study sample could be drawn if ancillary data were gathered on psychometric life history variables and other commonly studied life history traits, such as age at birth of first child and lifetime reproductive success (Bribiescas, 2001; Foo, Nakagawa, Rhodes, & Simmons, 2017; Gavrus-Ion et al., 2017; Woodley, Cabeza de Baca, Fernandes, Madison, Figueredo, Aguirre, 2017). Individual differences in these life history variables may precipitate variation in "pooled energy budgets" (Kramer & Ellison, 2010; Reiches et al., 2009) as well as shaping developmental niches (Stotz, 2017; cf. Lynch, 2016) that, further down the evolutionary-developmental trajectory, underlie the phenotypic covariation that we observed between family income, immune function and height.

More specifically, Latvia is a globally salient location in which to study relationships between organismal growth and resource availability. Latvia has represented an environment with a number of major disadvantages associated with low income and lack of economic stability especially between 1985 and 2010 (Cassis, 2011). These conditions may have a leading role in determining significant relationships between the availability of resources that influence ontogeny (McDade, 2005; McDade et al., 2008), the ability of the immune system to establish antibody protection against novel antigens (Zuin et al., 1992) and the ability of men to reach tall stature (Perkins et al., 2016). Lower resource availability has the potential to increase pathogen burden (Garcia and Blackwell, 2017) which may magnify trade-offs between immunity and other life history traits. This would make the effects predicted by the stress-linked immunocompetence handicap hypothesis more likely to appear (Muehlenbein and Bribiescas, 2005; Rantala et al., 2012).

Research on the influence of resource quantity and quality needs to be repeated using generations that were born under better conditions than the generation born around the time of the collapse of the Soviet Union in the early 1990s. We predict a lack of positive relationship between stature and the ability to produce higher antibody titers in young men born in the period of sustainable economic growth between Latvia's joining the EU in 2003 and the economic crises of 2008 because of better resource availability than experienced by our subjects. We encourage corresponding research in highly developed countries.

It is also important to note that a more careful selection of participants or a re-analysis of the data may increase the probability of finding significant relationships between height and immune function in populations where these relationships have not been found before. For example, a study done in Poland (Pawłowski et al., 2017) included a rather low number of participants with short stature which does not preclude a possibility for quadratic relationships especially between height and the strength of post-vaccination response, and between height and lymphocyte counts.

## 5 | CONCLUSIONS

Our results suggest a more complex relationship between height and immune function than found earlier (Krams et al., 2014; Pawłowski et al., 2017; Skrinda et al., 2014). While there is a positive association between height and antibody response, positive links also exist between height and income, and between income and antibody response. A detailed mediation analysis suggests that associations between height and antibody titers are indirect. This is because resource availability during ontogeny mediates both body growth *and* the development of the immune system (Georgiev et al., 2016; Sekiyama et al., 2018). Overall, the present study highlights the importance of resource availability and an optimal developmental niche (Stotz, 2017) to ensuring that young people receive the best possible start in life.

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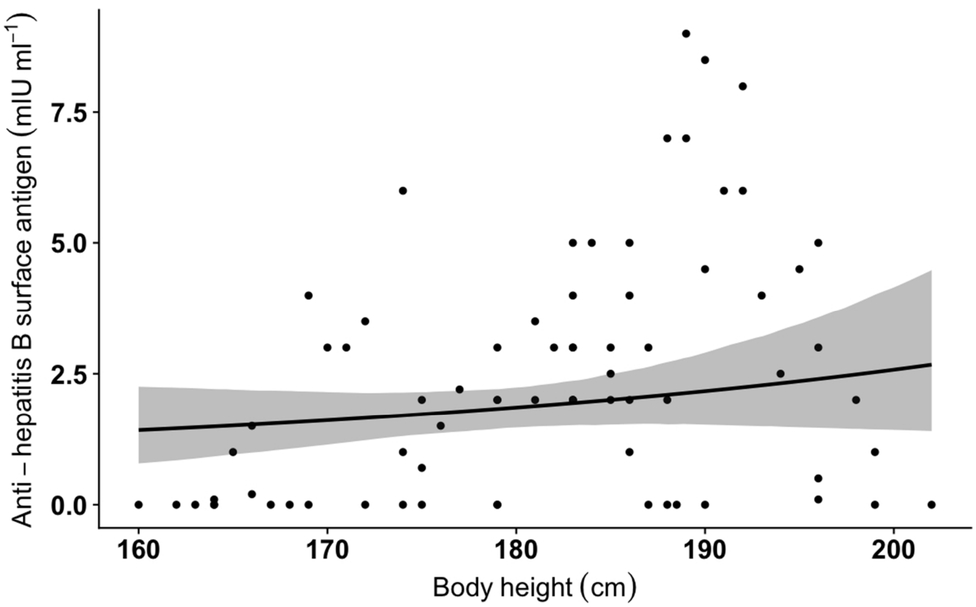
## Figure legends

FIGURE 1 A relationship between height and antibody response (n = 73). The solid line is the predicted antibody level for the height variable. The grey area designates confidence intervals calculated by the bootstrap method

FIGURE 2 A relationship between income and antibody response (n = 73). The solid line is the predicted antibody level for the income variable. The grey area designates confidence intervals calculated by the bootstrap method

FIGURE 3 A relationship between income and height (n = 73)

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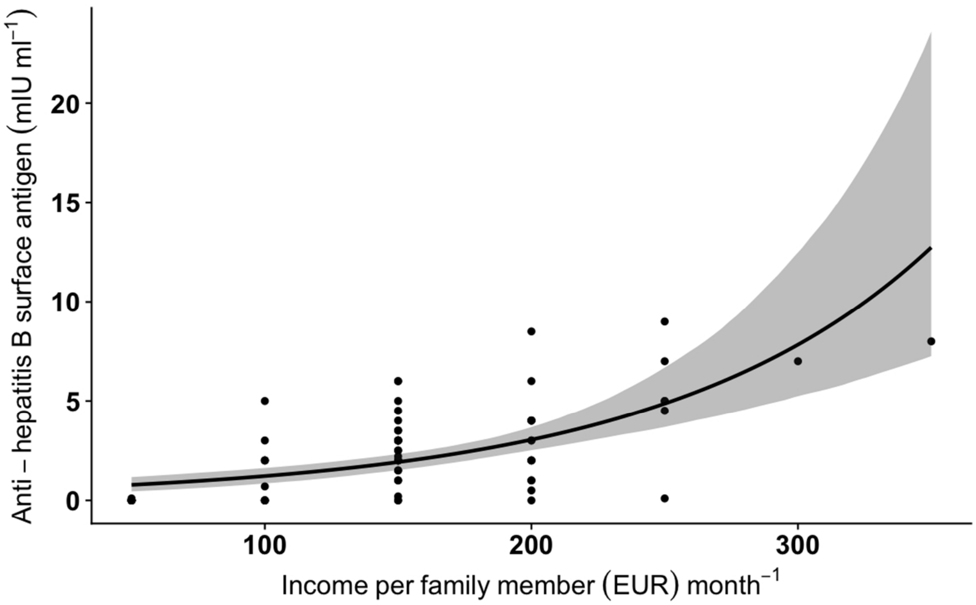


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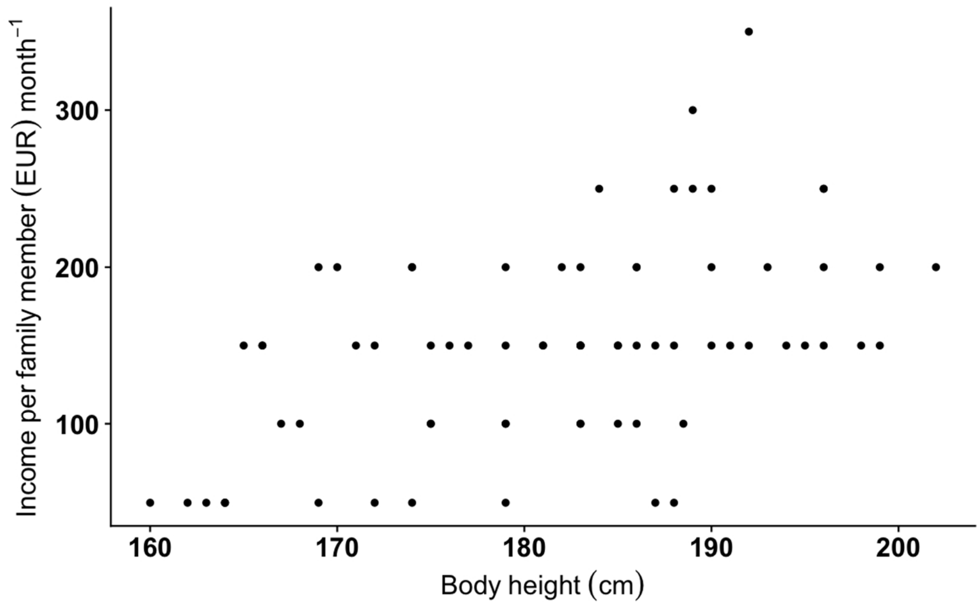


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**TABLE 1** The Tweedie compound Poisson generalized linear models show the effects of income and height on antibody response (n = 73)

| | Estimate | Standard error | *t*-value | *P* |
|---|---|---|---|---|
| Intercept | -3.389 | 1.912 | -1.773 | 0.081 |
| Income | 0.009 | 0.002 | 5.933 | < 0.0001 |
| Height | 0.015 | 0.011 | 1.349 | 0.182 |