



Sexual Selection and Extended Phenotypes in Humans

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How sexual selection maintains variation in attractive traits remains a complex problem in evolutionary biology (Kokko et al. 2006). Humans provide an additional challenge to testing sexual selection theories on morphology as many features of the human face and body can be altered, accentuated or extended culturally. Luoto (2018) tackles this additional layer of complexity by integrating theories spanning phenotypic plasticity, life history, behavioral ecology and sexual selection to discuss human extended phenotypes. A cross-national study using data on intelligence, population density, climate and economic complexity from 122 countries revealed that countries with more variable climates and greater population densities had greater economic complexity, while countries with higher parasite stress had lower economic complexity. A strong negative relationship was also reported between earlier age at first reproduction and economic complexity, which Luoto suggests represents life history trade-offs between energetic investment in extended phenotypes and reproduction. Luoto then outlines a research program for testing how sexual selection has shaped human extended phenotypes with a focus on their role in men's mating success. While this contribution represents an important advance in human behavioral ecology, some of the shortcomings of the past literature on sexual selection and human morphology are echoed. Here I outline some of these issues so that researchers may avoid their pitfalls when testing how sexual selection has shaped extended phenotypes.

Popular accounts of women's mate preferences, especially since Gangestad and Simpson's (2000) influential review, implicate trade-offs between heritable genetic benefits that enhance offspring survival and reduced paternal investment. Thus, women may bypass the costs associated with high quality (i.e. masculine) mates when selecting partners for short-term relationships, when their fertility is higher and under conditions of high pathogens (Gangestad and Simpson 2000). However, recent research using large samples of identical and non-identical twins reported that 38% of the variation in women's facial masculinity preferences was due to genetic variation while context-dependent factors including fertility, pathogen disgust and openness to short-term

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relationships explained less than 1% of the variance (Zietsch et al. 2015). Recent experimental research with large sample sizes have not reported causative effects of context-dependent factors on facial masculinity preferences (McIntosh et al. 2017; Dixson et al. 2018; Jones et al. 2018). Luoto suggests that women place a greater premium than men on phenotypic extensions in mate choice, so that men should invest more energetic resources in the production of phenotypic extensions than women, possibly to compensate for reduced physical attractiveness, particularly among populations with high than low resources (See hypotheses 11–14; Table 10). While these hypotheses are logically formed, they evoke mating strategies theory that, given the recent null findings in the field, would suggest such a framework may not be relevant to understanding how sexual selection has shaped male investment in phenotypic extensions.

An additional concern in past cross-cultural research on human mating strategies that employed cross-national analyses of the type presented by Luoto is that they often suffer from statistical issues such as multicollinearity, non-independence of data and inflating effects by using data aggregated at the national level to explain individual variation (Pollet et al. 2014). Thus, cross-national research reported women's facial masculinity preferences were predicted by lower national health indices and higher income inequality (Brooks et al. 2010; DeBruine et al. 2010). However, these analyses were restricted to the same dataset in which preferences were aggregated at the national level that likely obscured actual individual variation in mate preferences as a result of prevailing demographic factors (Pollet et al. 2014). Subsequent cross-cultural research using multi-level modelling found that women's preferences for facial masculinity were highest in populations with more urban development, higher human development indices and lower pathogen indices (Scott et al. 2014). Luoto acknowledges some of the shortcomings of cross-national datasets and undertook analyses split by geographic region to avoid issues of geographic non-independence. Nevertheless, should future research on extended phenotypes and sexual selection in humans employ cross-cultural approaches, multi-level modelling with large sample sizes of individuals from each society are recommended (Pollet et al. 2014).

Luoto draws attention to a modern goal in human behavioural ecology, which aims to understand how social and environmental contexts underpin plasticity in life history traits (Pepper and Nettle 2017). However, human beings are a difficult species for studying evolutionary theories of sexual selection derived from animal mating systems. Further, demonstrating genotype by environment ($G \times E$) interactions on mating behavior and life history variation within species is challenging and are best undertaken using model systems. For example, in the Australian black field cricket (*Teleogryllus commodus*), male investment in body size to defend territories and calling to attract mates can reduce survival (Hunt et al. 2004). Energetic resources during development are also allocated differently depending on the social environment. Males reared under lab conditions in which the density of male calls is higher mature later, are larger, and match their calling to that of the social environment, but die earlier (Kasumovic et al. 2016). This plasticity in developmental trajectories, which is associated with trade-offs between mating effort and life history, results in differential gene expression in the brains of male crickets (Kasumovic et al. 2016). While this level of experimental control and rigour is clearly not possible using human participants, cross-national correlational data are often interpreted as if they were controlled experiments without

genetic confounds. Thus, Luoto reports a negative correlation between cross-national levels of economic complexity and age at first reproduction as evidence of a life history trade-off between energetic investment in reproduction and extended phenotypes. However, age at first intercourse has a strong genetic component (Dunne et al. 1997), raising the possibility of a genetic confound in the cross-national association between age at first reproduction and economic complexity that could reflect non-adaptive mutational drift rather than localised responses to competing life history processes. This is not to say that individuals within populations never vary in the extent to which they invest in phenotypic extensions within their lifetime in response to prevailing environmental changes (Pepper and Nettle 2017). Rather, future research seeking to uncover whether investment in extended phenotypes varies as function of prevailing ecological or economic factors could benefit from testing $G \times E$ interactions with genetically informed datasets.

Luoto reviews how phenotypic extensions can enhance men's mating success using examples including luxury cars, apartments and clothing. With this in mind, recent research into the communicative role of men's facial hair can provide insights into how sexual selection operates at the interface of social and biological processes. While beardedness is markedly sexually dimorphic and develops due to genetically regulated androgen dependent processes, men can easily groom their facial hair at low costs to their health (Dixson et al. 2017a). Facial hair augments perceptions of men's age, masculinity, social dominance and aggressiveness (Dixson and Brooks 2013; Dixson and Vasey 2012) by enhancing masculine facial structure, particularly jaw size (Dixson et al. 2017a) and angry facial expressions (Dixson and Vasey 2012; Craig et al. *In Press*). Why men would choose to remove such a prominent cue of masculinity had until recently remained largely unexplored. Thus, analyses of facial hair fashions from 1842 to 1971 in Britain revealed that beards were more popular during periods when men were more abundant in the marriage market than women (Barber, 2001). This may reflect women's preferences for beards are under negative frequency dependent processes. Indeed, experimentally manipulating the frequency of facial hair causes stronger preferences for beards among women when beards are rare compared to when beards are common (Janif et al. 2014). Alternatively, men may be adjusting their masculine displays in response to prevailing intra-sexual competition. Cross-culturally, women's preferences for men's facial hair were stronger in larger cities, where beards were more common and average incomes were lower (Dixson et al. 2017b). Whether these patterns apply to other malleable phenotypic extensions such as clothing and cosmetics or investment in ownership of luxury status items would be interesting for future research to uncover.

Luoto's manuscript is an ambitious and important first step towards a more nuanced understanding of how social and ecological dimensions contribute to variation in mate selection in humans. The integration of theory from multiple sources is valuable and has the potential to drive new areas of research on how sexual selection has shaped cultural innovation in women and men. My hope is that this commentary can highlight some past pitfalls in the sexual selection literature on male attractiveness in order that they can be avoided in future research on sexual selection and extended phenotypes in humans.

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References

- Barber, N. (2001). Mustache fashion covaries with a good marriage market for women. *Journal of Nonverbal Behavior*, 25, 261–272.
- Brooks, R., Scott, I. M., Maklakov, A. A., Kasumovic, M. M., Clark, A. P., & Penton-Voak, I. S. (2010). National income inequality predicts women's preferences for masculinized faces better than health does. *Proceedings of the Royal Society of London B*. <https://doi.org/10.1098/rspb.2010.0964>.
- Craig, B. M., Nelson, N. L., & Dixon, B. J. W. (In Press). Sexual selection, agonistic signalling, and the effect of beards on men's anger displays. *Psychological Science*.
- DeBruine, L. M., Jones, B. C., Crawford, J. R., Welling, L. L. M., & Little, A. C. (2010). The health of a nation predicts their mate preferences: cross-cultural variation in women's preferences for masculinized male faces. *Proceedings of the Royal Society of London B*, 277, 2405–2410.
- Dixon, B. J., & Brooks, R. C. (2013). The role of facial hair in women's perceptions of men's attractiveness, health, masculinity and parenting abilities. *Evolution and Human Behavior*, 34, 236–241.
- Dixon, B. J., & Vasey, P. L. (2012). Beards augment perceptions of men's aggressiveness, dominance and age, but not attractiveness. *Behavioral Ecology*, 23, 481–490.
- Dixon, B. J. W., Lee, A. J., Sherlock, J. M., & Talamas, S. N. (2017a). Beneath the beard: do facial morphometrics influence the strength of judgments of men's beardedness? *Evolution and Human Behavior*, 38, 164–174.
- Dixon, B. J. W., Rantala, M. J., Melo, E. F., & Brooks, R. C. (2017b). Beards and the big city: displays of masculinity may be amplified under crowded conditions. *Evolution and Human Behavior*, 38, 259–264.
- Dixon, B. J., Blake, K. R., Denson, T. F., Gooda-Vossos, A., O'Dean, S. M., Sulikowski, D., & Brooks, R. C. (2018). The role of mating context and fecundability in women's preferences for men's facial masculinity and beardedness. *Psychoneuroendocrinology*, 93, 90–102.
- Dunne, M. P., Martin, N. G., Statham, D. J., Slutske, W. S., Dinwiddie, S. H., Bucholz, K. K., Madden, P. A. F., & Heath, A. C. (1997). Genetic and environmental contributions to variance in age at first sexual intercourse. *Psychological Science*, 8, 211–216.
- Gangestad, S. W., & Simpson, J. A. (2000). The evolution of human mating: trade-offs and strategic pluralism. *Behavioral and Brain Sciences*, 23, 573–587.
- Hunt, J., Brooks, R., Jennions, M. D., Smith, M. J., Bentsen, C. L., & Bussière, L. F. (2004). High-quality male field crickets invest heavily in sexual display but die young. *Nature*, 432, 1024–1027.
- Janif, Z. J., Brooks, R. C., & Dixon, B. J. (2014). Negative frequency-dependent preferences and variation in male facial hair. *Biology Letters*, 10, 20130958.
- Jones, B. C., Hahn, A. C., Fisher, C. I., Wang, H., Kandrik, M., Han, C., ... & O'Shea, K. J. (2018). No compelling evidence that preferences for facial masculinity track changes in women's hormonal status. *Psychological Science*, 29, 996–1005.
- Kasumovic, M. M., Chen, Z., & Wilkins, M. R. (2016). Australian black field crickets show changes in neural gene expression associated with socially-induced morphological, life-history, and behavioral plasticity. *BMC Genomics*, 17, 827.

- Kokko, H., Jennions, M. D., & Brooks, R. (2006). Unifying and testing models of sexual selection. *Annual Review of Ecology, Evolution, and Systematics*, 37, 43–66.
- Luoto, S. (2018). An updated theoretical framework for human sexual selection: from ecology, genetics, and life history to extended phenotypes. *Adaptive Human Behavior and Physiology*, 1–55.
- McIntosh, T. L., Lee, A. J., Sidari, M. J., Stower, R. E., Sherlock, J. M., & Dixson, B. J. W. (2017). Microbes and masculinity: does exposure to pathogenic cues alter women's preferences for male facial masculinity and beardedness? *PLoS One*, 12(6), e0178206.
- Pepper, G. V., & Nettle, D. (2017). The behavioural constellation of deprivation: Causes and consequences. *Behavioral and Brain Sciences*, 40, e31. <https://doi.org/10.1017/S0140525X1600234X>.
- Pollet, T. V., Tybur, J. M., Frankenhuis, W. E., & Rickard, I. J. (2014). What can cross-cultural correlations teach us about human nature? *Human Nature*, 25, 410–429.
- Scott, I. M., Clark, A. P., Josephson, S. C., Boyette, A. H., Cuthill, I. C., Fried, R. L., Gibson, M. A., Hewlett, B. S., Jamieson, M., Jankowiak, W., Honey, P. L., Huang, Z., Liebert, M. A., Purzycki, B. G., Shaver, J. H., Snodgrass, J. J., Sosis, R., Sugiyama, L. S., Swami, V., Yu, D. W., Zhao, Y., & Penton-Voak, I. S. (2014). Human preferences for sexually dimorphic faces may be evolutionarily novel. *Proceedings of the National Academy of Sciences*, 111, 14388–14393.
- Zietsch, B. P., Lee, A. J., Sherlock, J. M., & Jem, P. (2015). Variation in women's preferences regarding male facial masculinity is better explained by genetic differences than by previously identified context-dependent effects. *Psychological Science*, 26, 1440–1448.