Behavioral and Brain Sciences

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Self-protection as an adaptive female strategy

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Target Article

Cite this article: Benenson JF, Webb CE, Wrangham RW. (2022) Self-protection as an adaptive female strategy. *Behavioral and Brain Sciences* **45**, e128: 1–65. doi:10.1017/S0140525X21002417

Target Article Accepted: 1 November 2021
Target Article Manuscript Online: 8 November 2021
Commentaries Accepted: 11 February 2022

Keywords:
emotions; immunity and illness; insomnia; longevity and survival; neuroticism; *pain* and injury; reproductive success; sex differences; social interactions; stress and threat

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Abstract

Many male traits are well explained by sexual selection theory as adaptations to mating competition and mate choice, whereas no unifying theory explains traits expressed more in females. Anne Campbell's "staying alive" theory proposed that human females produce stronger self-protective reactions than males to aggressive threats because self-protection tends to have higher fitness value for females than males. We examined whether Campbell's theory has more general applicability by considering whether human females respond with greater self-protectiveness than males to other threats beyond aggression. We searched the literature for physiological, behavioral, and emotional responses to major physical and social threats, and found consistent support for females' responding with greater self-protectiveness than males. Females mount stronger immune responses to many pathogens; experience a lower threshold to detect, and lesser tolerance of, pain; awaken more frequently at night; express greater concern about physically dangerous stimuli; exert more effort to avoid social conflicts; exhibit a personality style more focused on life's dangers; react to threats with greater fear, disgust, and sadness; and develop more threat-based clinical conditions than males. Our findings suggest that in relation to threat, human females have relatively heightened protective reactions compared to males. The pervasiveness of this result across multiple domains suggests that general mechanisms might exist underlying females' unique adaptations. An understanding of such processes would enhance knowledge of female health and well-being.

1. Introduction

Across diverse, contemporary human societies, numerous sex differences appear in physiology, behavior, and experiences that often vary in magnitude depending on the culture (Archer, 2019; Berenbaum & Beltz, 2021; Geary, 2021; Hyde, 2005; Wizeman & Pardue, 2001; Wood & Eagly, 2002; Zell, Krizan, & Teeter, 2015). An evolutionary explanation for these differences relies on sexual selection theory.

Sexual selection occurs when one sex, usually the female, invests more in offspring, and the other sex, typically the male, invests more in mating competition (Darwin, 1871; Janicke, Häderer, Lajeunesse, & Anthes, 2016; Trivers, 1972). When applied to humans, sexual selection theory has produced many explanations and testable predictions regarding the reproductive benefits of males' competitive strategies, including direct competition, physical aggression, risk-taking, showing off, impulsivity, sensation-seeking, and resource accumulation (Archer, 2009, 2019; Walter et al., 2020). Because such behaviors can improve males' ability to succeed in mating competition, they constitute part of an optimal strategy for fitness maximization even when they reduce survival. Mating competition thus accounts for many "male traits" (those that are expressed more in males than females).

In contrast to male traits, evolutionary theorists have tended to explain female traits in a more piecemeal manner. At least four theories related to sexual selection commonly have been applied to understanding female traits: mating competition, social selection, parental investment, and (in humans) "staying alive" theory (SAT).

The mating competition component of sexual selection theory explains female traits as adaptations for either defeating other females in conflicts over mates or being chosen as mates by males (Janicke et al., 2016). In humans, a high-quality mate can enhance a woman's fitness through providing resources, protection, support, and/or good genes (Campbell, 2004). Human females' competitive strategies to attract high-quality males rarely involve direct competition, but instead rely more on self-promotion (Blake, Bastian, Denson, Grosjean, & Brooks, 2018; Puts, 2010) and indirect tactics including denigration of competitors' reputations and social exclusion (Archer, 2004; Campbell, 2004; Hess, Helfrecht, Hagen, Sell, & Hewlett, 2010; Reynolds, 2021).

Social selection theory applied to females emphasizes contests against other females for resources, territory, or allies (Clutton-Brock, 2007; Stockley & Bro-Jørgensen, 2010). Again, direct contests are relatively uncommon in humans (Campbell, 2004). Instead, human females frequently compete for resources and allies utilizing indirect tactics as in mating competition (Björkqvist, 1994; Burbank, 1987; Campbell, 2004; Jankowiak, Sudakov, & Wilreker, 2005; Rucas, 2017).

Parental investment theory focuses on how adults, typically females, provide optimal levels of care for their young (Trivers, 1972). The theory examines adaptations that maximize production and survival of offspring independent of mating relationships, including optimizing interbirth intervals, manipulating sex ratios, and aborting embryos or infanticide (Hrdy, 1981; Trivers, 1974; Trivers & Willard, 1973). Parental investment theory has been applied fruitfully to humans to explain diverse patterns of mothering (Hrdy, 1999).

Building on parental investment theory, Campbell (1999) proposed SAT. She posited that survival is more fitness-enhancing for females than males, and therefore that human females more than males evolved to avoid physical aggression and invest in alternative traits. Campbell (1999) emphasized "that lower rates of aggression by women reflect not just the absence of male risk-taking but are part of a positive female adaptation driven by the critical importance of the mother's survival for her own reproductive success" (p. 204). Campbell focused on fear as the critical mechanism that protects females from injurious forms of aggression, and found that females indeed tend to be more fearful than males.

Here we examine whether Campbell's theory has more general applicability by considering the hypothesis that compared to males, human females respond with greater protectiveness to other threats beyond aggression. We define threat as anything potentially damaging to an individual's survival.

Campbell's (1999) assumption that survival is more fitness-enhancing for females than males predicts that females tend to outlive males. In support, despite large cultural variations, in virtually every country women outlive men as shown in Figure 1 for 2020 (Roser, Ortiz-Ospina, & Ritchie, 2013). A similar tendency for females to live longer than males is found in mammals (Lemaître et al., 2020).

SAT also predicts that the sex difference in longevity has evolved at least partly because of the benefits that offspring receive from female care, assuming that females contribute more than males to offspring survival. Studies of contemporary societies from hunter-gatherers to Western, Educated, Industrialized, Rich, and Democratic (WEIRD) nations (Henrich, 2020) confirm females' greater investment in and contribution to offspring survival (Atrash, 2011; Hawkes, O'Connell, & Blurton Jones, 2018; Sear & Mace, 2008). According to Wood and Eagly's (2002) analysis of 186 geographically and culturally diverse non-industrial societies from the Human Relations Area Files, "all of the cultures in our review revealed an alliance between men and women in a division of labor, which appeared to be organized primarily to enable mothers to bear children and nurse and care for infants" (p. 718). Mothers were the principal caregivers of infants in 92% of these societies (and simultaneously of young children in 26–70% of these societies), whereas fathers and other men never were. Further, across six hunter-gatherer or horticulturalist societies, excluding nighttime co-sleeping, mothers took care of infants between 46 and 53% of the day and fathers between 0 and 6%, with older siblings, grandmothers, and others comprising the additional caregivers (Kramer, 2005).

Besides mothers, female kin, especially grandmothers and older daughters, most often helped mothers with childcare (Wood & Eagly, 2002). Grandmothers have been found to be particularly important for increasing grandchildren's survival, more so than grandfathers (Hawkes et al., 2018; Lahdenpera, Lummaa, Helle, Tremblay, & Russell, 2004; Sear & Mace, 2008). A high adaptive value of grand-mothering is suggested by eight mammalian species in which females contribute to caring for their grand-offspring, because females' lifespans in those species averaged 43% longer than males, compared to only 8% longer in related species without grand-mothering (Péron et al., 2019).

Older daughters also help mothers (Bove, Valeggia, & Ellison, 2002; Kramer, 2005; Whiting et al., 1988). Across 13 traditional societies, girls were more likely than boys to assist in direct care for younger siblings (Whiting et al., 1988). In six hunter-gatherer or horticulturalist societies, girls cared for younger siblings between 13 and 33% of the day, with boys childminding 1–14% of the day (Kramer, 2005). In WEIRD societies where children rarely care for younger siblings, girls more than boys cared for dolls ($d = 4.12$) (Davis & Hines, 2020). In non-human primates, preadult females also attend to and hold infants more than males do (Benenson, 2019).

These data support the idea that the greater longevity of females than males is an evolutionary response to women's larger role in childcare, such that at all ages selection tends to favor female survival. Thus, females and males confront different life history tradeoffs, with the sex that cares for offspring investing more in survival (Hamilton, 1966; Kirkwood & Rose, 1991; Trivers, 1972; Williams, 1966). Preliminary evidence in mammals also links higher female longevity with greater female, relative to male, parental care (Allman, Rosin, Kumar, & Hasenstaub, 1998).

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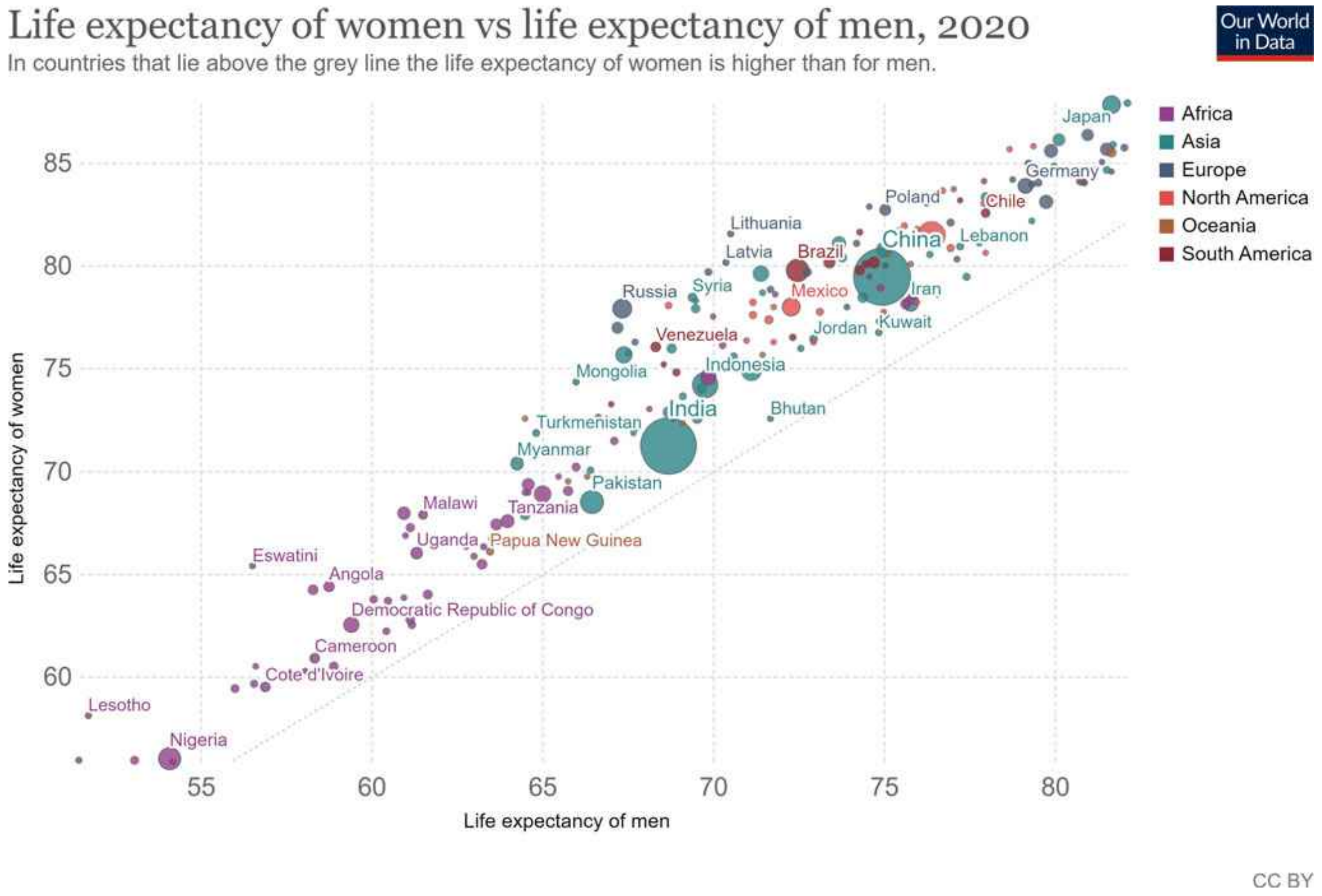

Figure 1. United Nations data for life expectancy by sex for 2020.
Source: UN Population Division (2019 Revision).
Note: Shown is the period life expectancy at birth measured in years.

To evaluate the applicability of Campbell's (1999) theory to threats beyond aggression, we searched for articles that analyzed sex differences in response to major threats to survival: internal and external physical dangers, social conflicts, personality styles, emotional reactions to threat, and threat-related clinical conditions. We surveyed highly cited reviews, meta-analyses, and articles that examined human sex differences with large samples from diverse countries, along with authoritative references such as the World Health Organization (WHO) and the Diagnostic and Statistical Manual of Mental Disorders 5th edition (DSM-V). We report sample sizes, effect sizes based on Hyde's (2005) cutoffs, and developmental effects when these were available. Because many fewer elderly men than women are alive thereby introducing confounds into sex-based comparisons, we focused on young and middle-aged adults. Further, because female investment in childcare increases sharply after puberty, we predicted increased magnitudes of sex differences following puberty and searched for evidence comparing children with adolescents. We included only high-quality datasets for each kind of threat and searched for inconsistencies with other published findings. Following Campbell (1999), we included only self-protective reactions to threat, rather than reactions that *increase* the potential for harm, such as impulsivity, sensation-seeking, risk-taking, direct aggression, or homicide which are well-known to be less common in females than males (Archer, 2019). Additionally, we reviewed Hyde's (2005), Zell et al.'s (2015), and Archer's (2019) meta-analytic summaries of sex differences to identify any additional protective reactions to threats or contrary findings. All sex differences we report were statistically significant unless otherwise stated.

We recognize that human sex is a multidimensional construct influenced by the continuing interplay of biological and environmental components and that the studies we found are limited by including only binary comparisons (Berenbaum & Beltz, 2021; Eliot, 2009; Fausto-Sterling, 2019; Hyde, Bigler, Joel, Tate, & van Anders, 2019). We also acknowledge that many sex differences in specific traits are small, so that sex stereotypes based on single traits mischaracterize the large overlap between the sexes (Hyde, 2005; Zell et al., 2015). Our goal is to suggest that many female-associated traits, which are often pathologized in comparison to male-related traits, can more appropriately be considered, like most evolved features, to enhance females' survival and reproductive success.

2. Protective responses to physical threat

According to our extension of SAT, females should protect themselves more than males in response to all physical threats. We therefore tested the hypothesis that females exhibit stronger defenses than males against pathogens, bodily damage, and environmental dangers.

Recent cross-cultural evidence shows that females were less likely than males to die from disease at every age. The major causes

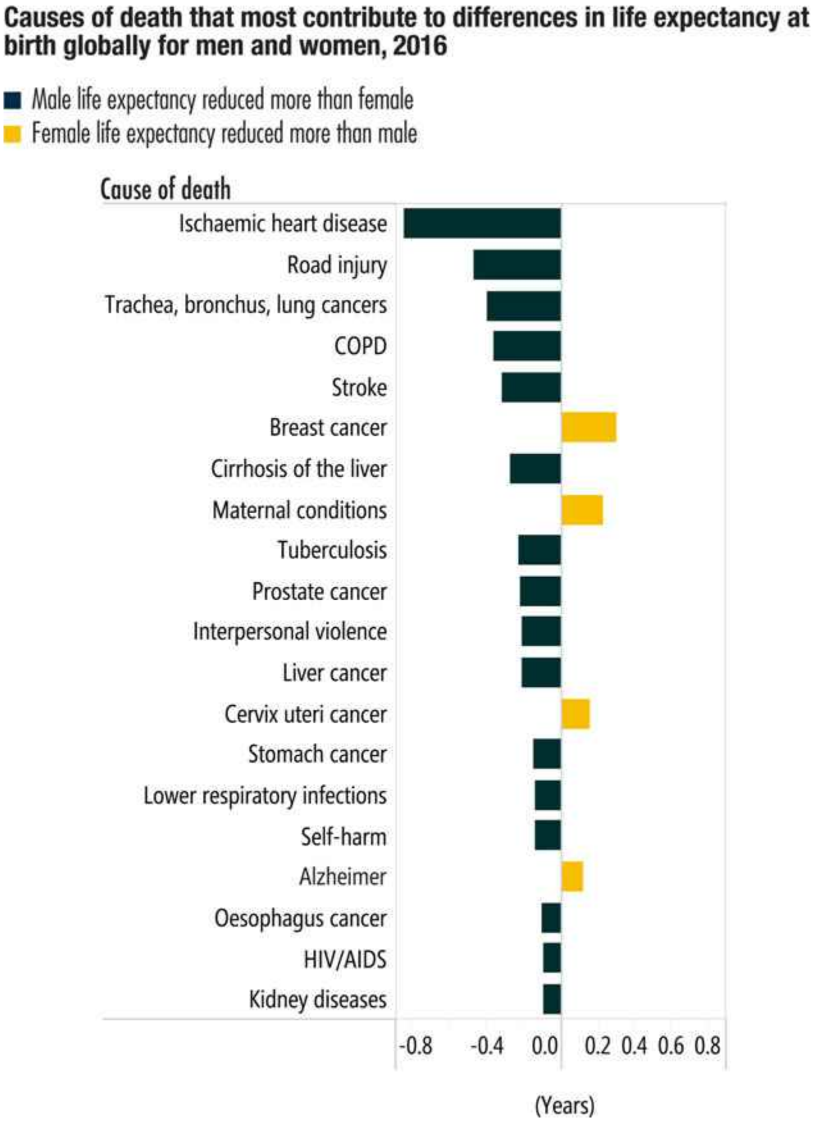

Figure 2. Sex differences in diseases that are major causes of death worldwide from the World Health Organization.
Source: WHO (2018) (*2*) and see (*4*) for composition of life expectancy. © Reprinted with permission from the World Health Organization.

of sex differences in mortality worldwide are shown in Figure 2 with disease the most common contributor (WHO, 2018).

Excluding reproductive-related conditions, the fatal illnesses that contributed most to reducing life expectancy afflicted females less frequently or later in life than males (Austad, 2006; Verbrugge, 1985). Thus, females were less likely than males to develop many diseases, including malaria, leptospirosis, schistosomiasis, brucellosis, rabies, leishmaniasis, pulmonary tuberculosis, hepatitis A, meningococcal and pneumococcal infections (Giefing-Kröll, Berger, Lepperdinger, & Grubeck-Loebenstein, 2015; Mihailova & Krams, 2018).

When females developed fatal diseases, they died later than males with small to moderate effect sizes. As examples, adjusting for age, worldwide in 2021 the odds of dying from lung (OR = 0.46), colorectal (OR = 0.68), and stomach (OR = 0.45) cancer were lower for women than men (WHO, 2021). In the United States in 2007, the age-adjusted odds of dying from cardiovascular disease (CVD) were lower for females than males (OR = 0.70) (Mosca, Barrett-Connor, & Kass Wenger, 2011). In the United States in 2010, females' age-adjusted death rate was lower than males' for 12 of the most frequent 15 diseases. Two were equal, while only Alzheimer's disease killed more women than men (Austad & Bartke, 2016). Mortality from the coronavirus disease-2019 (COVID-19) pandemic epitomizes the overall pattern: In 37/38 countries fewer women than men died (Scully, Haverfield, Ursin, Tannenbaum, & Klein, 2020) with an effect size (OR = 0.63) (Williamson et al., 2020). Sex differences in fatality rates from COVID-19 appeared even in mice (Scully et al., 2020). Overall, therefore, females are better protected than males from death by disease.

2.1. Immune defenses

Since immune activation is necessary for survival, SAT predicts that females should exhibit more effective immune responses than males. This prediction is upheld in vertebrates generally.

Across most vertebrate species, females are better able than males to defend themselves against a majority of environmental and vector-borne threats, including fungi, viruses, bacteria, parasites, and allergens, as well as internal threats such as tissue damage and tumors (Giefing-Kröll et al., 2015; Klein, 2000; Klein & Flanagan, 2016; Oertelt-Prigione, 2012; Ortona, Pierdominici, & Rider, 2019). Females' immune systems also respond better than males' to trauma, sepsis, and shock (Angele, Frantz, & Chaudry, 2006; Angele, Pratschke, Hubbard, & Chaudry, 2014). In response to injury, estrogen administration has been shown to promote healing by upregulating the immune system and reducing morbidity and mortality (Angele et al., 2014; Bösch, Angele, & Chaudry, 2018). The American National Health and Nutrition Examination Survey ($n = 38{,}000$) from 1988 to 2006 of demographically representative adults showed that women exhibited a stronger immune response than men, as indicated by a higher inflammatory rate, with a large effect size (OR = 4.17) (Yang & Kozloski, 2011).

The immune system functions in two waves (Roved, Westerdahl, & Hasselquist, 2017). First, the general, continually active, costly, rapid, innate part of the immune system responds to a new infection or inflammation. Second, cytokines released by the innate immune system ramp up the adaptive immune system through increased cell-mediated T and humoral-situated B cells which are capable of remembering specific antigens, thereby creating longer-term protection. The type of adaptive immune response varies with T-helper (Th) cells, with one type (Th1, Th2, or Th17) increasing at the expense of another. Th1 immune cells typically produce pro-inflammatory responses that clear infections, whereas Th2 cells produce anti-inflammatory immune responses.

Part of the reason for female mammals' stronger immune response is that the X chromosome encodes more immune-related genes than the Y chromosome, and females have two X chromosomes while males have only one (Klein & Flanagan, 2016). Further, in females, one X chromosome typically is randomly inactivated in each cell meaning that females are mosaics permitting increased transcription by both X chromosomes to contribute to immunity. Additionally, some X chromosomes escape inactivation also providing extra immunity (Takahashi & Iwasaki, 2021). In mice, experimentally adding an X chromosome to an XY individual to create an XXY individual increases longevity (Davis, Lobach, & Dubal, 2019).

Another reason for females' stronger immune defenses is their higher estrogen and lower androgen levels. Estrogens intricately regulate immunity by both stimulating and suppressing differing types of immune cells, while androgens generally reduce immune functioning (Foo, Nakagawa, Rhodes, & Simmons, 2017; Klein & Flanagan, 2016; Roved et al., 2017). Differing concentrations of estrogens can regulate the balance between T-helper cells-2 (Th2) and Th1 and Th17 cells. In contrast, androgens reduce Th2 and Th17 immune processes.

Estrogen levels are not solely responsible for enhanced immunity however, because even pre-pubertal girls activated stronger innate responses than boys, though some sex differences did not appear until puberty (Klein & Flanagan, 2016). After puberty, more components of both the innate and adaptive immune systems were upregulated in women than in men.

Some of the clearest evidence for females' stronger inflammatory response comes from reactions to vaccinations. In response to most vaccinations including influenza, pneumonia, hepatitis A and B, tetanus, diphtheria, measles, meningitis, rabies, yellow fever, and smallpox, especially after puberty, human females generally produced more antibodies, and experienced more side effects including fever, soreness, and redness, than males (Flanagan, Fink, Plebanski, & Klein, 2017; Klein, Jedlicka, & Pekosz, 2010). Immune responses were more suppressed in older individuals, but the suppression developed more slowly in women than men. Immune responses to vaccines were so much stronger in women than men that for a number of vaccines, half the dose of a vaccination in women caused the same level of antibodies as a full dose in men (Giefing-Kröll et al., 2015). While ceiling effects in vaccine efficacy obscure sex differences, when differences appeared, vaccines were more effective in females (Flanagan et al., 2017). However, when vaccine doses were too strong, females were more likely to die from the vaccine (Flanagan et al., 2011), as happened in some African infant inoculation campaigns (Aaby et al., 2020). Further, a higher concentration of circulating estrogens was positively related to stronger responses to vaccines in humans and mice (Aaby et al., 2020). Table 1 summarizes some of the human findings (Flanagan et al., 2017).

Results with mice demonstrated causality. In mice inoculated against H1N1, females produced more robust IgG and IgA antibodies and B cells and higher quality antibodies than males. When these mice were infected with H1N1, females became less sick, had a lower viral load in their lungs, and recovered more rapidly than males (Fink, Engle, Ursin, Tang, & Klein, 2018). Observations of people infected with COVID-19 similarly showed that women with higher antibody levels tended to be less sick (Takahashi et al., 2020).

Pregnancy illustrates the strength of the immune system in non-pregnant women. During pregnancy, myriad changes occur in the innate and adaptive immune systems that affect maternal and fetal responses to pathogens (Abu-Raya, Michalski, Sadarangani, & Lavoie, 2020). A pregnant woman's immune system must find an optimal way to balance ensuring survival of the genetically foreign fetus with protecting herself and the fetus from pathogens. One way this occurs is by downregulating Th1 cells producing pro-inflammatory cytokines. This switches the preponderance to Th2 cells producing anti-inflammatory cytokines. Sex hormones, including estrogens and progesterone, regulate the balance between Th1 and Th2 lymphocytes so that across pregnancy proinflammatory responses diminish and anti-inflammatory responses increase (Robinson & Klein, 2012).

The result is that pregnant women are more susceptible than non-pregnant women to, and/or suffer more severe, including fatal, reactions to infections from pathogens, including malaria, tuberculosis, influenza, hepatitis E, invasive pneumonia, herpes simplex virus, Ebola, and measles. In contrast, the severity of inflammatory diseases such as multiple sclerosis and arthritis is reduced (Abu-Raya et al., 2020). Increased maternal morbidity and mortality during pregnancy also occurred with recent severe acute respiratory viruses (H1N1, SARS, and MERS) (Schwartz, 2020), including COVID-19 (Zambrano et al., 2020).

Stronger activation of non-pregnant females' immune system however has a downside labeled "the health-survival paradox." Despite their greater longevity, women felt sicker and were diagnosed with more illnesses than men across North America and Europe, and in Egypt, China, Indonesia, Mexico, and the Tsimane of Bolivia (Alberts et al., 2014; Austad & Bartke, 2016; Christensen, Doblhammer, Rau, & Vaupel, 2009; Khadr & Yount, 2012; Macintyre, Ford, & Hunt, 1999; Mirowsky & Ross, 1995; Roved et al., 2017; Wheaton & Crimmins, 2016).

Older women from culturally diverse societies, including the Tsimane of Bolivia, Taiwan, Korea, Mexico, China, Indonesia, reported being sicker and weaker and were evaluated objectively by medical personnel and researchers to be in poorer health than men.

> "For instance, women in high-income countries are more likely than men to report difficulties in walking, climbing stairs, dressing, and other

Table 1 Sex differences in immune responses and adverse reactions to vaccinations over the lifespan.

Sex differences in acceptance, immune responses, and adverse reactions to vaccines in humans

Target group	Vaccine	Gender difference in acceptance	Sex difference in immune response	Sex and gender difference in adverse reactions	Age (years)
Children	Hepatitis B	Not defined	Greater in females	Not defined	<12
	Diphtheria	Not defined	Greater in females	Not defined	<2
	Pertussis	Not defined	Greater in females	Not defined	<2
	Pneumococcal	Not defined	Greater in females	Not defined	6–9
	Rabies	Not defined	Greater in females	Not defined	6–9
	Measles	Not defined	Greater in females or equivalent in both sexes	Increased in females	<3
	Malaria (RTS.S)	Not defined	Greater in females	Increased in females	<2
	Human papillomavirus	Less in males	Greater in females	Increased in females	5–17
Adults	Influenza	Less in females	Greater in females	Increased in females	18–49
	Hepatitis B	Not defined	Greater in females	Increased in females	18+
	Herpes virus	Not defined	Greater in females	Not defined	18+
	Yellow fever	Not defined	Greater in females	Increased in females	18+
	Rabies	Not defined	Greater in females	Not defined	18+
	Smallpox	Not defined	Greater in females	Not defined	18+
Aged adults	Influenza	Less in females	Greater in females	Increased in females	65+
	Td/Tdap	Less in females	Greater in males	Increased in females	65+
	Pneumococcal	Less in females	Greater in males	Increased in females	65+
	Shingles	Not defined	Not defined	Increased in females	65+

> common activities. In low-income countries, women report greater difficulties than men in a wide range of common activities such as bending over, pumping water, or walking a specified distance. In addition, women make more doctor visits, spend more days hospitalized, and take more medications than do men. Even in Russia, which has one of the largest sex differences in life expectancy in the world, with a male disadvantage of more than 10 years, males report better health and physical functioning at ages of 55 years and higher." (Austad & Batke, 2016, p. 42).

In twentieth-century American nationwide statistics, at all ages women experienced fewer fatal conditions than men, but suffered from more frequent daily symptoms, and more acute (except for injuries) and chronic and disabling conditions as diagnosed by doctors and in hospitals. The sex difference was largest during young adulthood, even after all reproduction-related conditions were excluded. Women reported more daily symptoms, more days with symptoms, more days in bed, more disability days, more health problems across more bodily systems, more prescription drug use, more alternative care visits, and more frequent discussions about their health problems with family and friends (Verbrugge, 1976, 1985, 1986, 1989).

The sex difference in the prevalence of immune activation increased at puberty but appeared by early childhood. In a large study of Norwegian adolescents ($n = 10{,}000$, ages 17–19 years), 47% of girls versus 21% of boys ($\mathrm{OR} = 3.34$) reported at least one weekly health complaint (Myrtveit Sæther, Sivertsen, Haugland, Bøe, & Hysing, 2018). Two weekly health complaints were reported by 30% of girls and 10% of boys ($\mathrm{OR} = 3.86$). Employing the Health Behaviour in School-Aged Children (HBSC) scale, a WHO study in 32 countries in Europe and North America plus Israel ($n = 1{,}500$ each nation at ages 11, 13, and 15 years, $n > 150{,}000$) found that girls reported poorer general health than boys at ages 11 ($\mathrm{OR} = 1.36$), 13 ($\mathrm{OR} = 1.68$), and 15 years ($\mathrm{OR} = 1.97$) (Cavallo et al., 2006). Likewise in the Avon Longitudinal Study of Parents and Children (ALSPAC) ($n > 13{,}900$), pregnant women in 1991–1992 in Southwestern England were recruited and later asked to report symptoms experienced by their 4–13-year-old children (Sweeting, Whitley, Teyhan, & Hunt, 2017). From 4 years onwards, more girls than boys experienced colds, cold sores, tonsillitis, urinary infections, earaches, headaches, stomachaches, worm infections, head lice or scabies, constipation, and eczema. Beginning at age 7, more girls than boys experienced rashes, and by 10 years, more girls than boys developed fevers, ear and eye infections, and were struggling with poorer overall health. In contrast, in childhood, boys were more likely than girls to suffer chest infections, breathlessness, wheezing, asthma, hay fever, pain in legs and joints, and diarrhea. After puberty, most of boys' excess health problems disappeared with girls then experiencing these problems equally or more frequently.

In summary, evidence supported the hypothesis that with the exception of pregnancy, human females mounted stronger and longer-lasting immune responses than males.

2.2. Preventing injury through the sensation of pain

Pain signals potential danger or actual damage typically following inflammation or trauma (Eisenberger & Lieberman, 2004). It therefore constitutes a critical self-protective warning mechanism and ongoing monitoring system that impels corrective action to protect an organism (Grahek, 2001). A heightened sensation of pain should reduce the prevalence of injury and repair damage from an already sustained injury by behaviorally removing or reducing pain-inducing stimuli, thereby enhancing survival. We therefore searched the literature to test the hypothesis that females experience greater pain than males.

Fillingim, King, Ribeiro-Dasilva, Rahim-Williams, and Riley (2009) reviewed clinical and experimental pain studies across diverse countries including rural Brazil, India, Nigeria, Turkey, as well as in European and North American nations. They found that in their daily lives, more women than men reported higher pain prevalence at all sites in the body in the prior week or day, including oral, abdominal, and head pain. Women experienced pain more than men from a variety of sources and across multiple bodily sites, including from cancer, neuropathic, musculoskeletal, and back pain. Likewise in a detailed study of 11,000 patients with 47 diagnoses in an American hospital, patient-reported or practitioner-rated pain scores were higher for women than men for the same diagnosis as pictured in Figure 3 (Ruau, Liu, Clark, Angst, & Butte, 2012).

The same sex difference appeared also for chronic, widespread pain. Mansfield, Sim, Jordan, and Jordan (2016) reviewed studies of chronic widespread pain in diverse countries including North and South America, the Middle East, Europe, Oceania, and Asia. Chronic widespread pain was reported more frequently by women than men on average by a 2:1 margin with large variation across ages and cultures and female:male ratios ranging from 1.06 to 4.80.

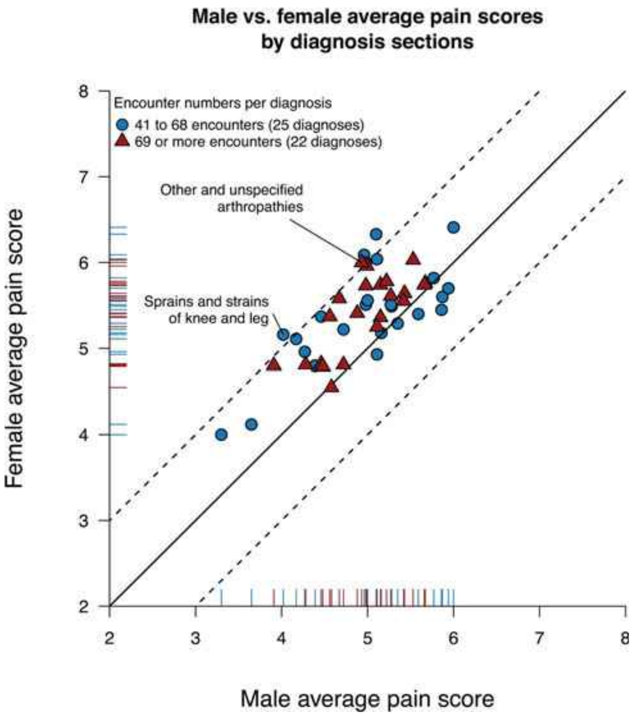

Figure 3. Average pain scores by sex for 47 conditions from one American hospital. © Reprinted from the Journal of Pain, 13/3, Ruau et al., Sex Differences in Reported Pain Across 11,000 Patients Captured in Electronic Medical Records, Pages 228–234, 2012, with permission from Elsevier.

Even during simple intramuscular injections, women experienced more pain than men (Fillingim et al., 2009). While this may be partially due to women's lower muscle density and tissue mass, even 5-year-old girls reported more pain than boys to venipuncture (Chambers, Giesbrecht, Craig, Bennett, & Huntsman, 1999).

Sex differences in pain emerge in childhood. The WHO HBSC study in 32 countries in Europe, North America, and Israel ($n >$ 150,000) found that more girls than boys experienced headaches at age 11, 13, and 15 years respectively (ORs = 1.44, 1.88, 2.70), stomachaches (ORs = 1.64, 2.00, 2.31), and backaches (ORs = 1.16, 1.24, 1.28) (Cavallo et al., 2006). Likewise, the English ALSPAC study found that beginning with the youngest children in their study (age 4 years), girls reported more headaches, stomachaches, and earaches than boys did (Sweeting et al., 2017). Chronic pain also was reported in childhood by females more than males (Fillingim et al., 2009).

Similar sex differences in responses to pain were found in mice and rats (Mogil, 2020). Rodent studies of the midbrain periaqueductal gray and the spinal cord showed that pain and analgesics are modulated differently in females than males (Shansky & Murphy, 2021).

In experimental studies that induce pain using identical stimuli, women consistently responded to bodily injury faster and endured it less long than men did across multiple bodily sites and modalities of inflicting pain (Fillingim et al., 2009). In a meta-analysis of pain threshold ($n >$ 1,600) and pain tolerance ($n >$ 41,500) for pressure, heat, electrical shock, and ischemic induced pain, women endured pain at a lower stimulus intensity ($d = 0.51$) and for a shorter time period ($d = 1.17$) than men did, yielding moderate to large effect sizes (Riley, Robinson, Wise, Myers, & Fillingim, 1998). The sex difference in pain diminished in old age but never disappeared (Girotti et al., 2019).

In experimental tests with children, a meta-analysis showed few sex differences (Boerner, Birnie, Caes, Schinkel, & Chambers, 2014). Overall, no sex differences were found in responses to pain intensity, and only 31% of studies found that girls exhibited lower pain thresholds than boys. Some specific types of pain, such as pain due to heat however, produced the same sex differences as in adolescents and adults.

In sum, adult females routinely experience greater pain than males. This suggests that a stronger experience of pain constitutes a female adaptation that functions to enhance survival through reducing injury. In support, the Global Burden of Disease findings showed that disability-adjusted lost years (DALYs) from all types of injuries were typically lower for females than males for ages 15–49 years, as displayed in Figure 4 (Haagsma et al., 2016).

The sex difference was smaller but in the same direction for children 0–14 years. From 1990 to 2017, the same sex difference for adults in DALYs appeared globally for child injuries from all causes except heat (James et al., 2020). Likewise, in the WHO HBSC study with 15-year-olds in 36 European and North American countries, girls reported fewer injuries overall than boys in the prior year and fewer physical fights (de Looze, Elgar, Currie, Kolip, & Stevens, 2019).

2.3. Countering nighttime threats through frequent awakening

Nighttime is a dangerous period because threats are not easily detected. Increased nighttime vigilance improves detection of

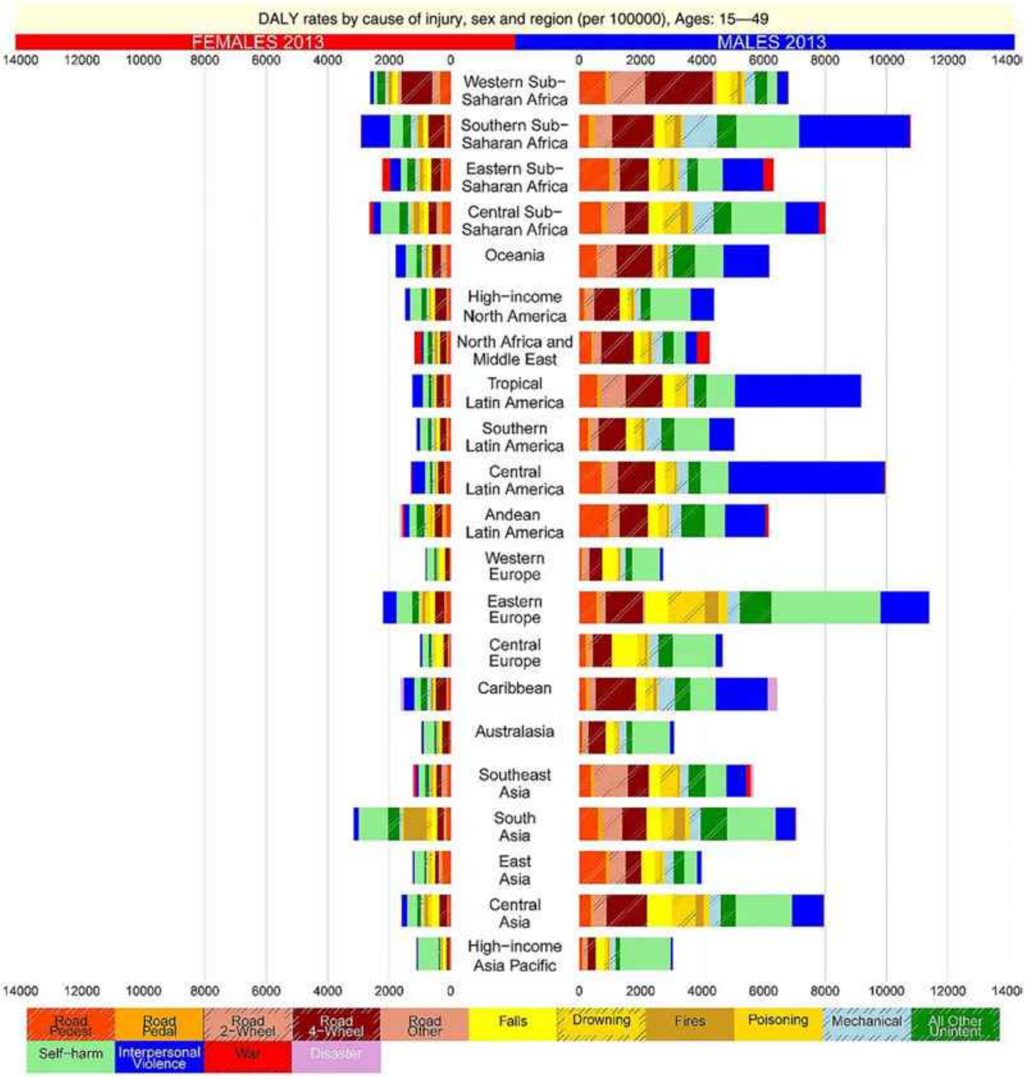

Figure 4. Disability-adjusted life year (DALY) by injury, sex, and region for ages 15–49 years from the Global Burden of Disease project. DALY rates per 100000. CC BY-NC 4.0

physical and social threats, including intruders, predators, and fire, that could elude identification during sleep. Accordingly, we tested the prediction from SAT that females are more attuned than males to nighttime threats.

We found that worldwide women reported being awake at night more often than men did. The American Society for Women's Health Research concluded that women's sleep differed objectively and subjectively from men's (Mallampalli & Carter, 2014): women experienced more slow wave sleep and less non-REM sleep than men. Women also experienced longer sleep latency and reported feeling sleepier than men. Further, across humans, mice, and rats, sex hormones affected females' more than males' sleep (Hajali, Andersen, Negah, & Sheibani, 2019; Mallampalli & Carter, 2014).

A meta-analysis ($n > 1.2$ million, ages 15–103 years) from diverse countries of sex differences in sleep disturbances illustrated the findings: In 26 of 29 studies, at all ages women reported more frequent nighttime awakening than men (risk ratio = 1.41) (Zhang & Wing, 2006). The Chinese Henan Rural Cohort Study ($n > 27{,}000$, ages 18–79 years) employing the Pittsburgh Sleep Quality Index found that females experienced lower sleep quality than males with effect sizes ranging from negligible to small for subjective sleep quality ($d = -0.20$), sleep latency ($d = 0.21$), sleep duration ($d = -0.03$), sleep efficiency ($d = -0.13$), sleep disturbance ($d = 0.15$), use of sleep medication ($d = 0.08$), daytime dysfunction ($d = 0.08$), and generally ($d = 0.22$) (Wang et al., 2019).

Globally, following puberty women had a 40% higher risk than men of developing insomnia during their lifetimes as depicted in Figure 5 (Mong & Cusmano, 2016).

Furthermore, a meta-analysis ($n > 180{,}000$) showed that more females than males experienced nightmares with negligible to small effect sizes in adolescents (Hedge's $g = 0.22$), young adults ($g = 0.26$), and in middle age ($g = 0.15$). The sex difference was not significant for children ($g = -0.03$), or >60 years ($g = 0.10$) (Schredl & Reinhard, 2011).

Although sex differences in nighttime awakenings were negligible to small for children, they increased with age and pubertal status. In the 32 country WHO HBSC survey, girls reported increasing sleep difficulties relative to boys at 11, 13, and 15 years of age (ORs = 1.13, 1.36, 1.56, respectively) (Cavallo et al., 2006). A study in Hong Kong ($n > 7{,}500$ ages 6–17 years) linked pubertal development to specific sleep disturbances (Zhang et al.,

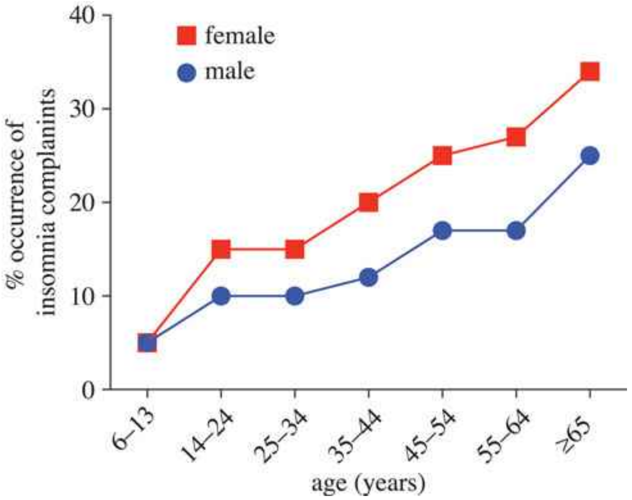

Figure 5. Prevalence of insomnia by sex and age. © Used with permission of The Royal Society from Sex differences in sleep: Impact of biological sex and sex steroids, Jessica A. Mong and Danielle M. Cusmano, 371, 2016, permission conveyed through Copyright Clearance Center, Inc.

2016). Children and adolescents, and their caregivers, reported that girls developed more overall insomnia, difficulty initiating sleep, and difficulty maintaining sleep than boys as they entered pubertal stage 4 on the Tanner scale, although they already had experienced more difficulties with early morning awakening as displayed in Figure 6.

Overall, evidence supported the hypothesis that females experienced more nighttime awakenings than males. This is consistent with the hypothesis that nighttime awakenings constitute a female adaptation that enhanced self-protection during an interval of heightened vulnerability.

We also noted that women were less likely than men to suffer from severe, potentially fatal sleep disorders including narcolepsy, obstructive sleep apnea, and hypoventilation (Hajali et al., 2019; Lévy et al., 2015). Furthermore, laboratory studies of sleep indicated that length, depth, and efficiency of sleep, including enhanced slow wave sleep and slow wave activity, were higher in women than men (Hajali et al., 2019; Mong & Cusmano, 2016; Suh, Cho, & Zhang, 2018). While these observations are limited to Western research, they suggest that females might compensate for their more frequent awakenings by maintaining a superior quality of sleep.

2.4. Miscellaneous physical threats

Innumerable external physical stimuli threaten survival. We tested the hypothesis, derived from SAT, that females would be more effective than males at avoiding or reducing such threats. We were able to locate evidence for three types of threat: hypothetical physical threats, long-term environmental degradation, and major disease outbreaks.

In the standardized International Affective Picture System (IAPS), participants evaluated the valence of photographs of nonhuman animals, scenes, and inanimate objects. In the United States, Germany, Switzerland, and China, girls and women reported stronger aversion than their male counterparts to all represented threats, including accidents, illness, pollution, and dangerous animals (Bradley, Codispoti, Sabatinelli, & Lang, 2001; Lang & Bradley, 2007) with moderate to large effect sizes in adults ($d = 0.36$) (Gomez, von Gunten, & Danuser, 2013), ($d = 0.55$) (Gong, Wong, & Wang, 2018) ($d = 0.43$ and 0.80) (McManis, Bradley, Berg, Cuthbert, & Lang, 2001), and in children ($d =$ 0.64 and 0.67) (McManis et al., 2001).

Similar sex differences have been found in response to environmental dangers. In the International Social Survey Programme (ISSP) administered in 1993 and 2000 in 26 countries from Asia, Eastern and Western Europe, North and South America, and Oceania ($n > 23{,}000$), women expressed more concern about the state of the environment than men did (Franzen & Meyer, 2010). Between 2009 and 2011, an expanded ISSP in 32 nations in Africa, Asia, Europe, North and South America, and Oceania ($n > 45{,}000$) showed that women exhibited more positive views than men toward protecting the environment, greater awareness of environmental problems, and more willingness to pay to correct environmental problems (Chan, Pong, & Tam, 2019).

With regard to major outbreaks of disease, a review with Asian, European, and North American participants ($n > 25{,}000$, 12 countries) showed that during disease outbreaks women reported being more likely than men to adopt avoidant and protective measures, including handwashing, wearing a mask, and quarantining (Bish & Michie, 2010). Across eight OECD countries ($n > 20{,}000$), women were more likely than men to have perceived COVID-19 as a serious health risk and to have complied with restraining public health rules (Galasso et al., 2020).

Nonetheless, women can be more reluctant than men to receive vaccines, most likely because of the more adverse side effects of vaccines in women than men (Flanagan et al., 2017). A review (37 studies, 15 diverse countries) of reactions to the 2009 strain of H1N1 influenza showed that both women in the general population and female health care professionals indicated they would be less likely than their male counterparts to be vaccinated (Bish, Yardley, Nicoll, & Michie, 2011). An explanation proposed by Bish et al. (2011) was that women tended to believe that the immediate negative effects of the vaccine outweighed its health benefits, consistent with greater side effects in women. A similar concern about negative effects might explain a meta-analysis ($n = 88$ studies) with African, Asian, Australian, European, North and South American samples, which found that women were 50% more likely than men to have adopted nonpharmacological prevention and avoidant measures in reaction to respiratory pandemics (OR = 1.49), whereas men were slightly more likely to take pharmaceutical protections (OR = 0.89) (Moran & Del Valle, 2016).

Overall, for the environmental threats we examined, women reacted more protectively than men with small to large effect sizes, consistent with a female adaptation for increasing longevity.

3. Protective responses to social threat

Social threat includes at least two distinct types: conflicts and isolation. Social conflicts can be physically dangerous, potentially leading to fights, reputation denigration, ostracism, expulsion, and even capital punishment (Boehm, 1999; Wrangham, 2019). Social isolation predicts psychological and physical morbidity and mortality in young, middle-aged, and elderly adults in a dose-dependent manner (Hawkley & Cacioppo, 2010). A meta-analysis of longitudinal studies ($n > 3.4$ million) showed that objective measures of both social isolation and feeling lonely predicted increased mortality (OR = 1.26–1.83) (Holt-Lunstad, Smith, Baker, Harris, & Stephenson, 2015). The longer the loneliness,

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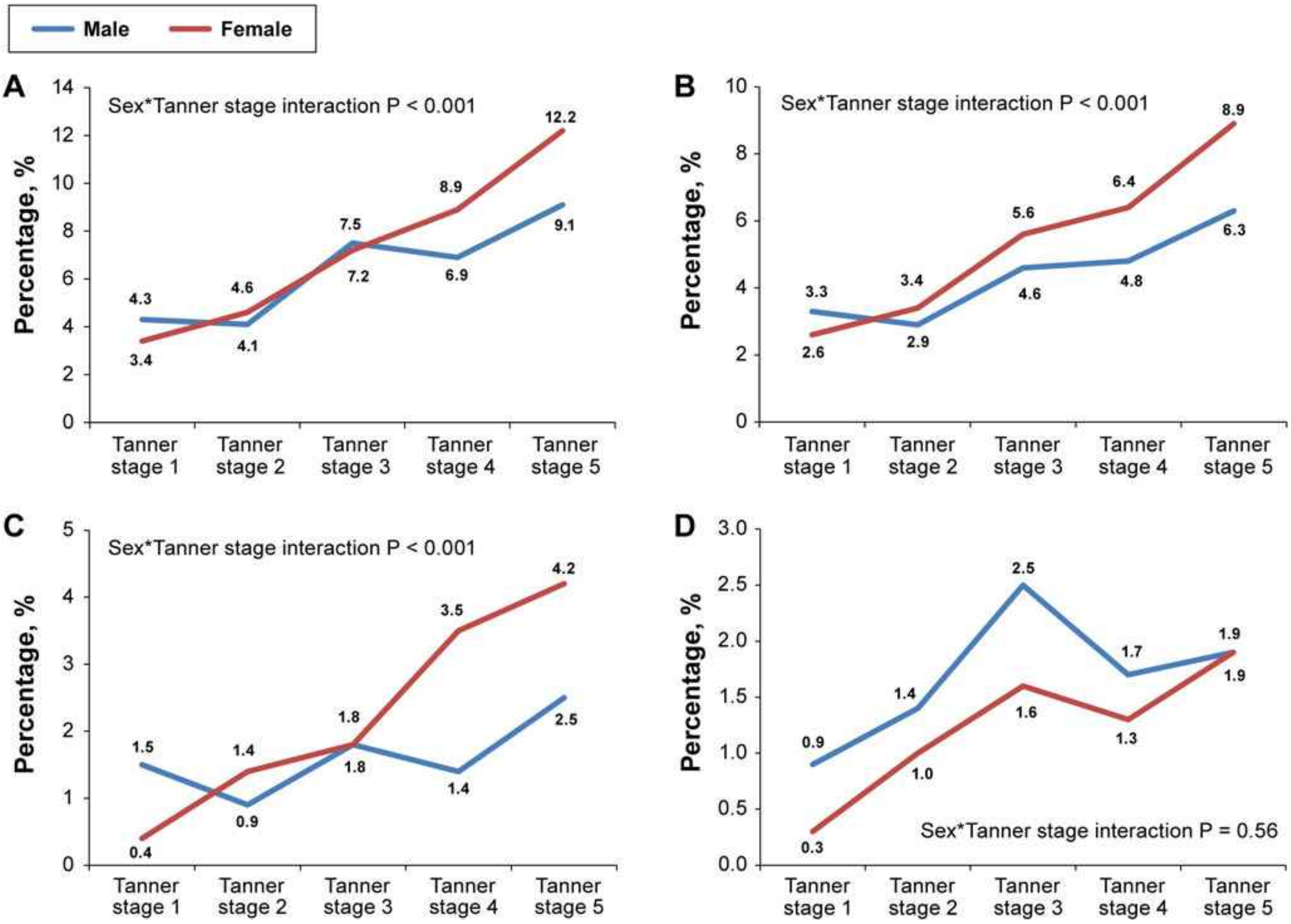

Figure 6. Rates of insomnia in Hong Kong by sex and Tanner stage for (A) overall insomnia symptoms, (B) difficulty initiating sleep, (C) difficulty maintaining sleep, and (D) early morning awakening. © Jihui Zhang et al., Emergence of Sex Differences in Insomnia Symptoms in Adolescents: A Large-Scale School-Based Study, Sleep, 2016, 39, 8, 1563–1570, by permission of Oxford University Press.

the greater the risk. Even experimentally inducing feelings of loneliness increased stress and feelings of danger (Holt-Lunstad et al., 2015).

Conversely, it is well known that social ties increase survival. A meta-analysis of longitudinal findings from Asia, Australia, Europe, and North America in community and patient samples ($n > 300{,}000$) showed that across sex, age, initial health status, and cause of death, social integration increased survival by 50%, and by 91% using multiple measures of integration (Holt-Lunstad, Smith, & Layton, 2010). Similarly, in a large study in Asia, Europe, and North America ($n > 7.5$ million), not being married increased all-cause mortality in both sexes, more for males (risk ratio = 1.46) than females (risk ratio = 1.22) (Wang et al., 2020).

SAT would predict that females tend to avoid conflicts and promote social ties more than males do. We found relevant evidence for four strategies that reduce negativity in interactions and facilitate positive connections, namely smiling, politeness, emotion identification, and avoidance of confrontations.

3.1. Smiling

Evidence indicates that women smile more than men with small to moderate effect sizes. A meta-analysis of 162 studies ($n >$ 100,000, 13 countries, 6 continents) reported greater smiling by women from adolescence through old age in every country ($d =$ 0.41) (LaFrance, Hecht, & Paluck, 2003). Sex differences were greater in same-sex pairs ($d = 0.48$) than mixed-sex pairs ($d =$ 0.35). Sex differences also were larger in contexts with greater social tension ($d = 0.47$) than little tension ($d = 0.20$), and when participants were unfamiliar ($d = 0.45$) rather than familiar ($d =$ 0.24). This suggested that an important function of smiling was to reduce threats from other individuals. Prior meta-analyses also concluded that women's smiles more than men's function to reduce social tension (Hall & Halberstadt, 1986).

Computerized coding likewise showed that women smiled more than men. Analyses of photographs of Asian, Black, and White New York City residents posted to Instagram and Twitter ($n > 15{,}000$) demonstrated that the more females in a picture, the more smiling occurred as coded by automated software (Singh, Atrey, & Hegde, 2017). Software similarly found that in Argentina, Brazil, China, Colombia, France, Germany, India, Japan, Mexico, Peru, Russia, the United Kingdom, and the United States ($n > 740{,}000$), when watching television advertisements women smiled more than men (McDuff, Girard, & El Kaliouby, 2017). Sex differences in smiling however were not found in children (Else-Quest, Hyde, Goldsmith, & Van Hulle, 2006).

3.2. Politeness

SAT would predict that females would be more likely than males to speak politely since this should reduce interpersonal conflicts. We tested the hypothesis that females more than males employed polite language.

Evidence indicated that females exhibited greater politeness than males with small to moderate effect sizes. In a meta-analysis in primarily WEIRD countries ($n > 3{,}500$, 29 studies), women used more tentative language (hedges, expressions of uncertainty, intensifiers, and tag questions) than men ($d = 0.23$), which the authors interpreted as seeking the listener's consent (Leaper & Robnett, 2011). Ethnographic reports from Africa, Europe, North and South America, and Oceania also reported that girls and women used more tentative speech than boys and men by employing more qualifiers, euphemisms, and apologies, and speaking with less assertiveness, more agreement, higher numbers of softeners and compliments, and greater supportiveness and modesty (Brown & Levinson, 1987; Coates, 2015; Guadagno & Cialdini, 2007; Haas, 1979; Holmes, 1989; Lakoff, 1975; Locke, 2011).

The same type of sex difference in the use of language has regularly been found in early childhood. In a meta-analysis of speech forms in WEIRD cultures (46 studies, $n > 2{,}600$), girls made more general affiliative comments ($d = 0.26$) than boys which was even stronger in unstructured contexts ($d = 0.58$) (Leaper & Smith, 2004). Ethnographic reports in 13 non-WEIRD societies likewise indicated that in middle childhood girls use more prosocial and less egoistic dominance in their speech (Whiting et al., 1988).

3.3. Identification of others' emotions

Accurately identifying another's emotions facilitates interactions by enhancing understanding of the actor's emotional state. SAT would predict that females would be more likely than males to accurately identify another's emotions.

Studies utilizing primarily pictures or short videos of non-verbal facial, bodily, and vocal behavior consistently demonstrated that from early in life females detected social signals more accurately than males did with small to moderate effect sizes. A meta-analysis (75 studies, 1923–1978) with WEIRD and non-WEIRD societies showed that girls and women were better able than boys and men to accurately detect others' non-verbally expressed emotions ($d = 0.40$) (Hall, 1978). A follow-up review demonstrated that across cultures, ages, and target sex, girls and women were better able than boys and men to accurately detect the emotional valence of non-verbal facial and bodily behaviors, as well as verbal intonation and prosody ($d = 0.41$–0.54) (Hall, Carter, & Horgan, 2000). A more recent meta-analysis showed that in 67% of 32 studies, women were more accurate than men in identifying the valence of emotions, whereas no sex differences occurred in the remainder (Forni-Santos & Osório, 2015). Similarly, an online study ($n > 7{,}300$, ages 18–75+ years) employing the Penn Emotion Recognition Test with happy, sad, angry, and fearful faces showed that women more accurately identified emotions across the lifespan ($d = 0.41$) (Sasson et al., 2010).

Importantly, women were particularly proficient at detecting negative emotions, though the specific negative emotions were not always consistent across studies and the effect sizes were small. In a large meta-analysis ($n > 79{,}000$), which encompassed several of the prior meta-analyses with children through adults in nations from Africa, East and Southeast Asia, Europe, North and South America, and including New Guinea, Taiwan, and Tibet, an overall female advantage was found in accurate recognition of emotional reactions to threat ($d = 0.24$) and of positive emotions ($d = 0.19$) (Thompson & Voyer, 2014). For specific emotions, the effect sizes were highest for anger ($d = 0.25$), sadness ($d = 0.24$), and fear ($d = 0.22$), then slightly lower for happiness ($d = 0.18$), disgust ($d = 0.17$), and surprise ($d = 0.15$), indicating that females were more accurate than males at all ages in decoding emotional signals of threat from non-verbal expressions.

In an Emotion Recognition Test ($n > 42{,}000$, ages 11–78 years) conducted in seven South American nations, plus Mexico, Austria, Germany, Spain, Switzerland, and the United States, females were more accurate than males at identifying emotions ($d = 0.22$) (Merten, 2005). For specific emotions however, the sex difference was significant only for anger, fear, and sadness (not for disgust, joy, or surprise). In three online studies ($n > 1{,}900$) in which subjects rated static facial and dynamic bodily emotions in less than one second, women recognized disgust and sadness significantly more accurately than men did, but not anger, fear, or happiness (Connolly, Lefevre, Young, & Lewis, 2019).

McClure (2000)'s meta-analysis of 58 studies of facial emotion processing in infancy through adolescence likewise demonstrated that girls were more accurate than boys at identifying emotions. The effect size was smaller in older children and adolescents ($d = 0.18$) than in infants ($d = 0.70$) however, which may be attributable to the earlier maturity of infant females than males (McClure, 2000).

Thus overall we found that females are reported to accurately identify others' emotions more than males.

3.4. Avoidance of confrontation

SAT would predict that females are more likely than males to avoid confrontations and facilitate positive interactions. We found two forms of confrontation with systematic evidence: direct competition and face-to-face aggression.

Evidence indicates that direct competition and aggression are less common in females than males with moderate to large effect sizes. Direct competition has been systematically examined both in economic games and sports. A standardized economic game was created in which individuals chose to either compete against others or work alone with equal expected payoffs (Niederle & Vesterlund, 2007). In WEIRD and non-WEIRD societies, across tasks, group size, and sex of opponents, two reviews concluded that girls and women were less likely than boys and men to compete against others (Klege, Visser, Barron, & Clarke, 2021; Sutter, Zoller, & Glatzle-Rutzler, 2019). Based on Klege et al. (2021), we calculated effect sizes for 33 studies with adults ($d = 0.43$) and 12 studies with children ($d = 0.55$).

Similar evidence comes from sports. Throughout known history, cross-culturally women have participated less than men in competitive sports (Craig, 2002; Leibs, 2004). In a geographically and culturally diverse sample of 50 societies, of 248 sports documented, males participated in 95% of the sports and females in 20%, whereas no sex differences existed in participation in amusements (Deaner & Smith, 2013). In the detailed American Time Use Survey (2003–2010) of activities in the past 24 hours ($n > 112{,}000$), 0.64% of females and 2.69% of males ($d = -0.92$) participated in team sports, and 1.29% of females and 4.45% of males participated in 1:1 sports ($d = -0.95$), whereas no sex differences occurred in exercise (Deaner et al., 2012). Whether in the context of sports or simply informal interactions, ethnographic evidence from Africa, Canada, Europeans, Native Americans, and in Oceania also described the less competitive and conflictual relationships of girls and women compared with boys and men (Locke, 2011).

Similar to findings on sex differences in direct competition, females were found to engage in less verbal ($d = -0.30$) and physical ($d = -0.59$) confrontation than males (Archer, 2019), with moderate effect sizes. Although most studies came from Asia, Europe, and North America, ethnographic reports provided the same conclusion. Despite large cultural variation, females engaged in less frequent and severe direct aggression than males did (Fry, 1998; Locke, 2011). The sex difference in direct aggression occurred across diverse cultures by age 2 years and continued through adolescence (Maccoby & Jacklin, 1974). In non-human primates as well, females typically engaged in less intense physical aggression than males (Sabbi et al., 2021; Smuts, 1987).

Thus evidence from smiling, politeness, emotion identification, and avoidance of direct confrontation indicated that females invested more than males in reducing social conflicts and protecting social bonds. This result is consistent with the finding from 70 countries with student and adult samples ($n > 75{,}000$) that women evaluated the "preservation and enhancement of the welfare of people with whom one is in frequent personal contact" as more important than men did ($d = 0.19$–0.36) (Schwartz & Rubel, 2005).

4. Personality style as a response to threat

Neuroticism consists of a wide range of negative behaviors, moods, emotions, and thoughts. One component of neuroticism, focused on worry and feelings of vulnerability, has been associated with reduced morbidity and mortality (Weiss & Deary, 2020). Because worry and feeling vulnerable are consistent with promoting self-protective behaviors toward threats, we interpreted SAT as predicting that females should report higher neuroticism than males.

The conclusion from four large cross-cultural studies is that beginning in adolescence, women exhibit higher neuroticism than men. First, in a study of university students ($n > 17{,}500$), neuroticism was defined as worrying, tension, nervousness, depression/blue, moodiness, uncalm in tense situations, easily upset, and not relaxed/handling stress poorly. In 49 of 55 countries, women reported more neuroticism than men did, whereas in no country did men report higher neuroticism than women ($d = 0.40$). Figure 7 displays effect sizes for sex differences in personality styles from world regions with neuroticism showing small to moderate sex differences (Schmitt, Realo, Voracek, & Allik, 2008).

Second, in an online study with individuals primarily from Australia, Canada, Ireland, New Zealand, and the United States ($n > 1.2$ million, ages 10–65 years, 70% Caucasian, 8% Asian, 6% African, 6% Hispanic), neuroticism was defined by worrying, not remaining calm in tense situations, being depressed/blue, and being moody (Soto, John, Gosling, & Potter, 2011). Overall neuroticism, and sub-clinical levels of anxiety and depression, differed by sex with females' rates increasing in early adolescence and remaining high during their peak reproductive years as displayed in Figure 8.

Third, a study of US adults ($n > 320{,}000$) defined neuroticism as being anxious, angry, depressed, self-conscious, immoderate, and vulnerable. As before, women, particularly during their reproductive years, described themselves as more neurotic than men ($d = 0.40$) with the anxiety ($d = 0.56$) and vulnerability ($d = 0.54$) scores yielding the greatest sex differences (Kajonius & Johnson, 2018).

Finally, in a classic study of personality in 24 highly diverse countries with university students and adults, women rated themselves as more neurotic than men: more vulnerable ($d = 0.28$–0.44), anxious ($d = 0.32$–0.43), self-conscious ($d = 0.22$–0.30), depressed ($d = 0.17$–0.24), impulsive ($d = 0.11$–0.23), and angry/hostile ($d = 0.09$–0.19), although sex differences in angry/hostile were not always significant (Costa, Terracciano, & McCrae, 2001).

In childhood, as depicted above, sex differences in neuroticism began after age 10 years. Facets of neuroticism, particularly anxiety, however, demonstrated sex differences even earlier (Soto et al., 2011).

In summary, beginning in adolescence females consistently report higher neuroticism than males, with small to moderate effect sizes. The greater neuroticism of post-pubertal females conforms to the prediction from SAT, suggesting that neuroticism functions to protect females more effectively than males from a diversity of threats.

5. Emotions: immediate reactions to threat

Emotional reactions to threat constitute critical signals that promote staying alive (Darwin, 1872; Ekman & Oster, 1979; Lazarus, 1991). Six basic emotions have been identified because they appear across diverse cultures, occur in other primates, and emerge in childhood (Ekman & Cordaro, 2011). Four of these (fear, disgust, sadness, and anger) are considered responses to threat, whereas two (joy and surprise) are not. Each basic emotion arising in response to a threat is believed to produce a unique aversive signal that promotes a defensive action aimed at removing or avoiding the threat.

Assuming that emotional responses to threat promote survival, SAT would predict that females should experience these emotions more than males. We therefore tested the hypothesis that females experience more fear, disgust, sadness, and anger than males.

5.1. Fear

Fear enhances survival by motivating an individual to withdraw from potentially life-threatening danger (Ekman & Cordaro, 2011; Lazarus, 1991). Campbell (1999) predicated SAT on female's greater fear of physical aggression, while our extension of SAT predicts that females would exhibit greater fear than males to any threat.

Cross-cultural studies confirm that women tend to display greater fear than men. Archer's (2019) review reported greater fearfulness for adult females than males with small to large effect sizes ($d = 0.07$–1.16). Additionally, when university students ($n = 5{,}000$) from 11 countries were asked to rate the fearfulness of 52 stimuli organized into social, agoraphobic, bodily, and animal categories, women in every nation reported greater fearfulness to every category ($d = 0.02$–0.90) (Arrindell et al., 2004). Further, in 1975–1980 when university students from 28 diverse countries were asked whether either sex was better described by various adjectives, women were characterized as more fearful than men in every country (Williams & Best, 1990).

In the International College Student Data (ICSD) survey ($n > 6{,}000$, 39 countries), students reported how frequently and intensely they experienced different emotions. Women described more frequent and intense fear than men ($d = 0.31$) (Lucas & Gohm, 2000). In two studies, one with an Australian sample of students, kin, and friends ($n > 2{,}100$), and a second with an international sample of students from 41 countries ($n > 6{,}500$), women

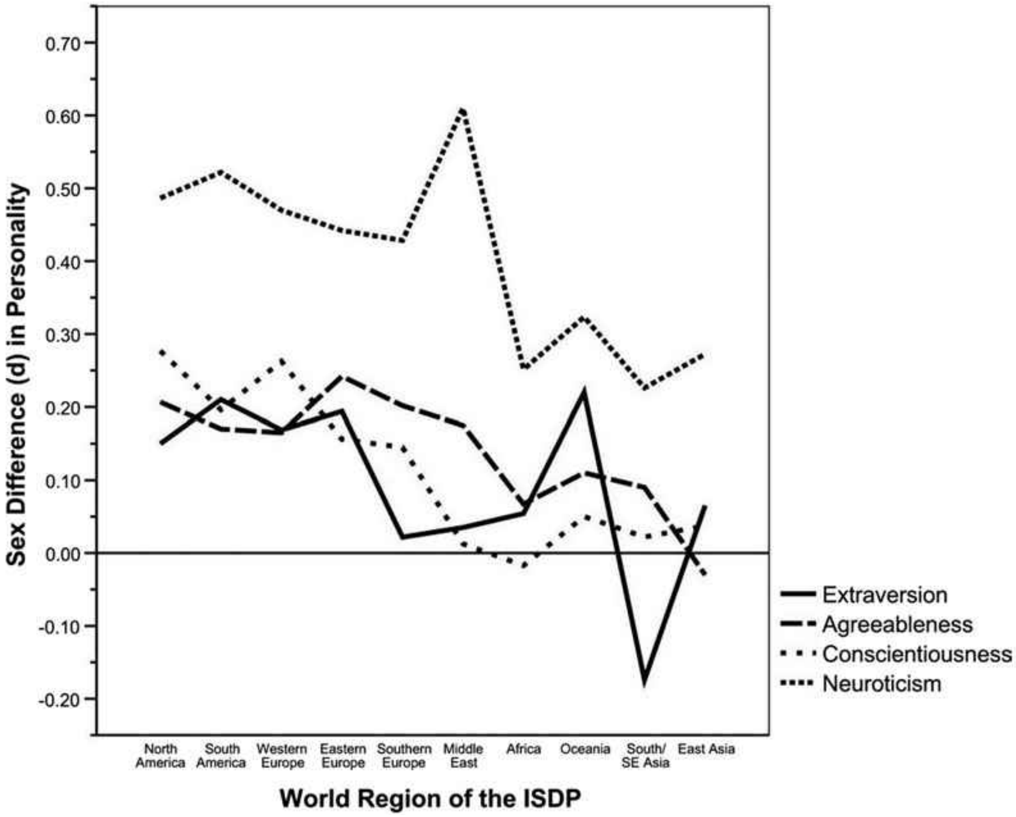

Figure 7. Magnitudes of sex differences in neuroticism by world region based on the International Sexuality Description Project. © Reprinted with permission of the American Psychological Association.

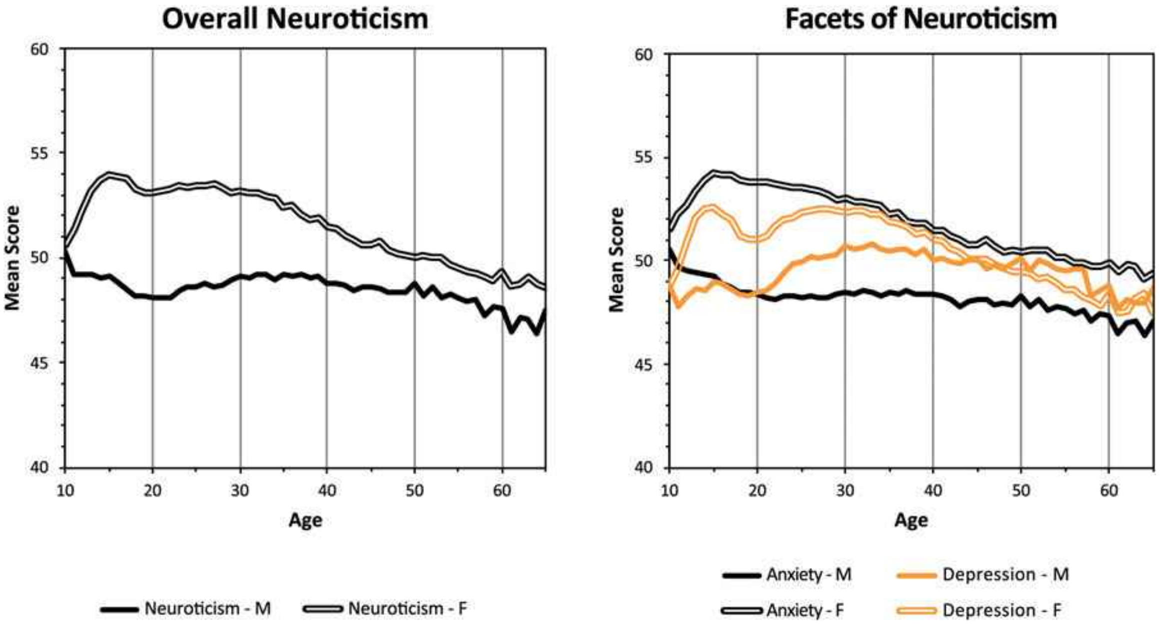

Figure 8. Sex differences in neuroticism by age in a large English-speaking sample. © Reprinted with permission of the American Psychological Association.

reported more frequent fear in the past month in Australia (d = 0.14) and in the international sample (d = 0.17) and more intense feelings of fear in the international sample (d = 0.26) (Brebner, 2003).

A small effect has also been found in children. In a cross-cultural meta-analysis (n > 4,500, 3 months–13 years), girls displayed greater fear than boys (d = 0.12) (Else-Quest et al., 2006).

5.2. Disgust

Like fear, disgust is believed to enhance survival by producing withdrawal from potentially life-threatening danger (Ekman & Cordaro, 2011; Lazarus, 1991). Classically, disgust arises in response to illness-causing objects, such as feces, vomit, mucous, signs of severe illness, rotting flesh, and other potentially contaminating stimuli. Additional, less well-known forms of disgust include sexual, animal, and moral disgust. Experiencing greater disgust or revulsion is directly linked with higher germ avoidance (Hartmann & Siegrist, 2018), immediately increased immune activation (Schaller, Miller, Gervais, Yager, & Chen, 2010; Stevenson et al., 2012), and disease avoidance (Curtis, Aunger, & Rabie, 2004; Oaten, Stevenson, & Case, 2009). Since disgust acts as a mechanism for self-protection, SAT would predict that females would experience greater disgust than males.

We found that across varied disgust-producing stimuli, females experienced more disgust than males, with small to large effect sizes. In an online cross-cultural study ($n > 390{,}000$, 67 countries), women were more distressed than men about lack of physical/spiritual purity and contamination (Atari, Lai, & Dehghani, 2020). Likewise, on the BBC science website ($n > 39{,}000$), children and adults evaluated which of two paired images evoked more disgust. Across ages and continents, females were more likely than males to rate the image designed to appear as if it could transmit disease as more disgusting than its disease-free twin (Curtis et al., 2004). In another online study ($n > 6{,}100$, ages 20–69 years, 10 nations, 5 continents), researchers examined disgust ratings for animal flesh, poor hygiene, human contamination, mold, decaying fruits, fish, decaying vegetables, and living contaminants (Egolf, Hartmann, & Siegrist, 2019). Across countries women's disgust ratings were greater than men's ($d = 0.12$–0.37). Similarly, participants from Canada, England, and the United States ($n > 2{,}500$, mean age 28 years) evaluated degree of disgust toward five targets. Women provided higher ratings than men for animal disgust ($d = 0.82$), sex disgust ($d = 0.70$), hygiene disgust ($d = 0.48$), food disgust ($d = 0.44$), and lesion disgust ($d = 0.31$) (Curtis & de Barra, 2018). Sexual stimuli produced some of the largest sex differences. Women experienced greater disgust than men to sexual stimuli ($d = 0.60$–1.54) (Al-Shawaf, Lewis, & Buss, 2018).

Sex differences in disgust appeared in childhood. As described in the large paired comparison study which began at age 7 years, even the youngest girls exhibited greater disgust than boys (Curtis et al., 2004).

5.3. Sadness

Sadness is believed to result from the loss of someone or something important to one's life (Ekman & Cordaro, 2011; Lazarus, 1991). Attachment theory posits that sadness or grief represents separation distress from a support figure (parent, spouse, ally) or from someone with close genetic ties (child, twin) (Archer, 2008; Bowlby, 1980). Loss of a relationship partner can threaten the bereaved's survival (Holt-Lunstad et al., 2015) or reproductive success (Archer, 2008) and often leads to withdrawal. Unlike with fear and disgust however, with sadness the loss often has already occurred, and withdrawal is gradual rather than sudden. Withdrawal is believed to protect the bereft individual who likely has lost a current or future ally, and to help elicit support from others (Lomas, 2018). On the assumption that sadness functions to reduce the impact of a threatening factor (the loss of a relationship partner), SAT would predict that females would experience greater sadness than males.

Based on self-reports, females were found to exhibit more sadness than males, with small effect sizes. In the IAPS, standardized photographs depicting illness generated more sadness in women than men (Bradley et al., 2001). In the 39 nation ICSD survey, women reported more frequent and intense sadness than men did ($d = 0.26$) (Lucas & Gohm, 2000). Likewise, women reported more frequent sadness in Australia ($d = 0.17$) and the 41 country international sample ($d = 0.16$), and more intense feelings of sadness in Australia ($d = 0.19$) and the international sample ($d = 0.28$) (Brebner, 2003).

Higher self-reports of sadness could in theory be accounted for by women's greater willingness to report emotion. To examine this possibility, in 1990 researchers interviewed a demographically representative sample of Americans ($n > 2{,}000$, ages 18–90 years) (Mirowsky & Ross, 1995). When asked the number of days in the prior week they felt sad, women reported more days of sadness than men. Then, participants were asked how much they hide their emotions. At every level of emotional reserve, women reported experiencing greater sadness than men, strongly suggesting that the sex difference in reported sadness was not due to a reporting bias.

Limited evidence suggests girls are sadder by adolescence. In a demographically representative American sample ($n > 21{,}000$, ages 14–18 years), girls felt sadder than boys (Moeller, Brackett, Ivcevic, & White, 2020). Likewise, when Swedish adolescents ($n > 1{,}000$, ages 16–18 years) in 49 classrooms were asked how frequently they experienced sadness, 35% of the girls versus 8% of the boys reported feeling sad either "fairly often" or "very often" (OR = 6.19) (Wiklund, Malmgren-Olsson, Öhman, Bergström, & Fjellman-Wiklund, 2012). In childhood, sex differences in sadness may not exist or are negligible. In a meta-analysis ($n > 2{,}300$), in 11 of 16 studies in early and middle childhood exhibited girls greater sadness than boys, but the sex difference was not significant and negligible in size ($d = 0.10$) (Else-Quest et al., 2006).

Evidence also indicated that females cry (weep) more than males, with moderate to large effect sizes. Crying is often associated with sadness, although it can also serve as a release from emotion and as a means of soliciting support (Rottenberg, Bylsma, & Vingerhoets, 2008; Vingerhoets & Scheirs, 2000).

In the International Study of Adult Crying (ISAC) ($n > 5{,}500$) conducted in 37 nations across six continents, university students were asked how easily and how frequently they had cried in the past month (Van Hemert, van de Vijver, & Vingerhoets, 2011). In every country, women reported crying more easily ($d = 1.11$) and more recently ($d = 0.94$) than men. Another meta-analysis (15 studies) found that women reported crying more frequently, intensely, and for longer intervals than men across cultures, including Israel, Japan, and the United States (Vingerhoets & Scheirs, 2000). Similarly, across Australia, Croatia, the Netherlands, Thailand, and the United Kingdom ($n > 800$, ages 18–40 years), women reported crying more frequently ($d = 0.74$) and intensely ($d = 0.45$) than men (Sharman et al., 2019). Ethnographic reports from diverse cultures similarly report that the loss of a relationship partner causes sadness and weeping, and more so in women than men (Palgi & Abramovitch, 1984). Sex differences in crying are not reported before adolescence (Vingerhoets & Scheirs, 2000).

5.4. Anger

Anger occurs after a personal goal has been obstructed, often by a specific perpetrator who purposefully wishes to harm a victim and/or her/his associates (Ekman & Cordaro, 2011; Lazarus, 1991). Unlike fear, disgust, and sadness however, anger activates approach, not withdrawal. A further contrast is that although anger-motivated responses can reduce a threat through avoidance, they can also increase the risk of being injured through approaching a perpetrator (Sell, Tooby, & Cosmides, 2009). This means that whether anger functions as self-protection will vary with the context. Anger should be more self-protective if it enhances avoidance of a perpetrator, but less self-protective if it motivates close engagement or cycles of retaliation. Experiencing anger without approaching the perpetrator however should highlight the danger of future interactions with specific perpetrators, thereby enhancing survival.

SAT therefore would predict that females would feel angrier than males toward perpetrators, though only when the approach was suppressed. Even though the prototype of an angry person is a man (Kring, 2000) most likely because larger individuals face lower likelihood and costs of retaliation (Sell et al., 2009), we tested the hypothesis that females feel angrier than males.

Evidence suggested at most a negligible effect size indicating females experienced more anger than males (Archer, 2004; Kring, 2000). However, no studies distinguished simple anger from anger tied to aggression. A meta-analysis of 11 countries found a non-significant effect for females to feel angrier than males ($d = 0.04$) (Archer, 2004). In the ICSD study, women reported more frequent anger than men ($d = 0.08$) (Lucas & Gohm, 2000). Likewise, in Brebner's (2003) Australian and international samples, women reported experiencing anger more frequently than men did both in Australia ($d = 0.06$) and the international sample ($d = 0.05$). Women also reported greater intensity of anger in the international sample ($d = 0.14$). In Mirowsky and Ross (1995) American study, anger was defined as "feeling annoyed with things or people," "feeling angry," and "yelling at someone." Women reported feeling angrier than men, and "yelling at someone" more than men did. Sex differences in experiencing anger have not been found in children (Potegal & Archer, 2004).

In conclusion, evidence supported the hypothesis that females experienced more fear, disgust, and sadness than males did. Results did not support an overall sex difference in anger but anger could not be separated from approaching a perpetrator. When a sex difference did arise however, women experienced more anger than men.

6. Clinical conditions: extreme self-protective reactions to threat

Some clinical conditions are believed to be non-adaptive exaggerations of normal adaptive reactions to stress (Del Giudice, 2018; Nesse, 2005). If self-protectiveness is an adaptive female strategy, then clinical conditions constituting extreme self-protectiveness to threats should be more prevalent in females than males. We therefore tested whether extreme forms of physical, social, emotional, and generalized reactions to threat occur more frequently in women than men.

6.1. Autoimmune diseases

As we reviewed above, non-pregnant women tend to exhibit stronger immune responses than men including enhanced Th2 reactions. Extrapolating from this result, we reasoned that more females than males would develop extreme immunoenhancing conditions. We therefore searched the literature to test the hypothesis that more females than males develop extreme immune reactions.

The prediction was supported by evidence that globally, women are more likely than men to develop systemic autoimmune diseases (AD) which are linked to proinflammatory responses with moderate effect sizes (Ji, Sundquist, & Sundquist, 2016; Moroni, Bianchi, & Lleo, 2012; Purnamawati et al., 2018) and diminish in severity during pregnancy (Abu-Raya et al., 2020). Of 81 ADs identified worldwide, 47 afflict females more than males, 22 are more common in males, and 9 exhibit no sex difference (Hayter & Cook, 2012). Despite large cultural differences, overall 6.4% of females and 2.7% of males develop an AD (OR = 2.46) with onset most common between 20 and 29 years. The more prevalent an AD, the higher the proportion of females who develop it, with women comprising 78% of those with ADs (Hayter & Cook, 2012). Whereas many female-preponderant ADs are believed due to enhanced Th2 responses, in male-preponderant ADs, Th1 reactions often are stronger (Fairweather, Frisancho-Kiss, & Rose, 2008). Precipitating factors for all ADs include infections or other types of diseases or trauma (Nielsen, Kragstrup, Deleuran, & Benros, 2016). Results therefore are consistent with a female adaptation that promotes immunoenhancing reactions to physical threat.

6.2. Pain disorders

Evidence reviewed above demonstrated that females experience more ordinary pain than males. According to the idea that clinical conditions are non-adaptive extensions of well-adapted responses, extreme pain reactions should be found more often in females than in males.

We found two examples for which cross-cultural evidence is available, migraine headaches and fibromyalgia (FM), both of which were experienced by more females than males. The Global Burden of Diseases report finds that despite large national variations, worldwide 18.9% of women and 9.8% of men experienced migraine headaches (OR = 2.15) with women ages 15–49 years most affected (Stovner et al., 2018). The most common precipitating factor was external stress, including odors, foods, weather, pain to the neck or head, or emotional trauma (Peroutka, 2014; Woldeamanuel & Cowan, 2017).

FM consists of chronic, severe, widespread pain in at least 11 of 18 points in the joints, muscles, and spine. Worldwide, 4.2% of females and 1.4% of males (OR = 3.09) developed FM (Queiroz, 2013). Onset of FM typically followed a stressor, such as an accident, surgery, infection, or emotional trauma, and was accompanied by sleep disturbance, fatigue, memory, and concentration problems, along with depression and anxiety (Galvez-Sánchez, Duschek, & del Paso, 2019; Häuser, Thieme, & Turk, 2010). Prevalence ratios of migraine and FM showing moderate effect sizes were consistent with the hypothesis that a female adaptation exists for heightened experience of pain.

6.3. Sleep disorders

Prior evidence showed that females experienced more nighttime awakenings than males, which is plausibly an adaptive response. More extreme, non-adaptive nighttime awakenings were therefore also expected to occur more often in females than in males. We therefore tested whether more females than males developed conditions with severe nighttime awakening.

In line with this prediction, we found that more women than men experienced severe sleep disturbances with small to moderate effect sizes. Although no sharp distinction separates nighttime awakenings from a severe sleep disorder (Suh et al., 2018), analyses of major DSM-V clinical conditions showed a female:male prevalence ratio of 1.4 for insomnia disorder and 1.5–2 for restless leg syndrome, which disrupts sleep, as well as a higher female prevalence for nightmare disorder (Hartung & Lefler, 2019). A meta-analysis ($n > 18{,}500$) further confirmed a female preponderance for restless leg syndrome (OR = 1.63–2.22) (Ohayon & Roth, 2002). Additionally, a detailed study in Hong Kong ($n > 8{,}500$) found women were more likely than men to experience nightmares ⩾3 times/week (OR = 2.10) (Li, Zhang, Li, & Wing, 2010).

Furthermore, major sleep disruptions including day-night reversals were associated with clinical conditions with a female preponderance (Lashley, 2003). These included responses to infections, many autoimmune conditions (systemic lupus erythematosus, multiple sclerosis, rheumatoid arthritis), pain-related disorders (migraine, FM), and as described below, anxiety disorders, major depression, post-traumatic stress disorder, and chronic fatigue syndrome. Prevalence ratios of severe sleep disruption were consistent with the thesis that because a female adaptation exists for being especially attuned to nighttime threats, females were also vulnerable to having extreme responses that are likely maladaptive.

6.4. Separation disorder

We have presented evidence that females were more likely than males to avoid social confrontations and to become more distressed about relationship partners' well-being. A more extreme version of this response would consist of becoming extremely distressed about the loss of relationship partners. We therefore tested whether more females than males develop conditions characterized by excessive concern for the maintenance of relationships. We found one condition with cross-cultural evidence that clearly fit this criterion: separation anxiety disorder. Separation anxiety disorder includes severe distress at being away from an attachment figure along with persistent worry about negative events befalling attachment figures.

Examining 18 DSM-IV mental disorders ($n > 72{,}000$, across Africa, the Americas, Asia, Europe, the Middle East, and the Pacific), the WHO World Mental Health Survey (WMHS) study found that lifetime prevalence of separation anxiety disorder was more common in females than males with a small effect size (OR = 1.6), whereas the reverse was true for antisocial disorders (Seedat et al., 2009). Similarly, in analyses of the DSM-V categories, separation anxiety disorder was more common in females than males, while males suffered more from antisocial disorders (Hartung & Lefler, 2019; Holthausen & Habel, 2018; Shear, Jin, Ruscio, Walters, & Kessler, 2006). A demographically representative survey in the United States ($n > 14{,}000$) likewise showed that by the end of early childhood and throughout life females were more likely than males to have experienced separation anxiety disorder (OR = 2.2) (Shear et al., 2006). Reported rates of separation disorder are thus consistent with a heightened female adaptation for maintaining relationships.

6.5. Anxiety disorders

Evidence reviewed above demonstrated that females of all ages were more likely than males to experience fear in response to threats. More persistent and intense fear reactions would accordingly be expected to develop in females than males. We therefore tested whether more females than males developed conditions characterized by severe fear.

Anxiety disorders are specific or generalized worries and fears about potential threats often accompanied by unpleasant physical sensations, including increased heart rate and shaking. The worldwide WHO WMHS study showed a higher prevalence for females than males of anxiety disorders with small effect sizes, including panic disorder (OR: 1.9), generalized anxiety disorder (OR: 1.7), agoraphobia (OR: 2.0), social phobia (OR: 1.3), specific phobia (OR: 2.0), separation anxiety disorder (OR: 1.6) as mentioned, and any anxiety disorder (OR: 1.7) (Seedat et al., 2009). Other estimates of the female:male ratio of global prevalence of anxiety disorders were 1.9 (Remes, Brayne, Van Der Linde, & Lafortune, 2016) with the DSM-V analysis finding a ratio of 2:1 (Hartung & Lefler, 2019). Thus, anxiety disorders conform to the hypothesis that they represent exaggerated versions of responses that would be adaptive if produced at an appropriate level.

6.6. Major depression and suicide attempts

Earlier we showed evidence that females were more likely than males to experience sadness. Extrapolating from this produces the prediction that more females than males should develop an extreme form of sadness: depression. We tested this hypothesis.

Major depression consists of an array of uncomfortable emotional and physical symptoms including sadness, feelings of worthlessness, reductions in activity and energy levels, changes in appetite and sleep, and difficulty thinking. In 80% of cases, depression is precipitated by stress (LeMoult, 2020). A meta-analysis of sex differences in major depression across six continents ($n > 1.7$ million, ages 12–70+ years) showed a higher female prevalence with a moderate effect size (OR = 1.95) (Salk, Hyde, & Abramson, 2017). The DSM-V analysis reported depression to be 1.5–3 times more common in women than men (Hartung & Lefler, 2019).

Major depression likely plays a role in suicide attempts. Suicide attempts however may be not only an exaggeration of depression, but also an adaptive request for help across diverse societies (Syme, Garfield, & Hagen, 2016). Although cross-culturally women were less likely than men to commit suicide (Alothman & Fogarty, 2020; WHO, 2014b), women were more likely than men to attempt suicide, beginning in early adolescence (Freeman et al., 2017; Lenz et al., 2019; WHO, 2014b). Maximal rates of non-fatal self-injuries for females occurred between 10 and 24 years (OR = 1.72). Females were still more likely than males to attempt suicide between 25 and 44 years (OR = 1.29), but the sex difference became negligible at older ages (Nock et al., 2008). A meta-analysis of suicide attempts by 12–26-year-olds further found that in 23 of 24 studies girls were more likely than boys to attempt suicide (OR = 1.96) (Miranda-Mendizabal et al., 2019). Effect sizes range from small to moderate. The higher rates of depression and lower success of female suicide attempts can be interpreted as females being more invested in self-protection, in line with SAT.

6.7. Psychiatric disorders incorporating disgust

We found previously that females were more likely than males to experience disgust in response to potentially contaminating stimuli. We therefore tested the idea that more extreme forms of disgust would also be more common in females than males.

We found that disgust is integral to three psychiatric illnesses: animal phobias, contamination-related obsessive–compulsive disorders with continual washing (OCD), and blood-injection-injury (BII) phobia which can include fainting. All three of these illnesses were more common in women than men (Arrindell, Mulkens, Kok, & Vollenbroek, 1999; Davey, 2011; Mathis et al., 2011; Olatunji, Cisler, McKay, & Phillips, 2010; Wani & Ara, 2014). Disgust has also been associated with other serious psychiatric problems that are more prevalent in women than men, including eating disorders, agoraphobia, and female sexual dysfunction (Hartung & Lefler, 2019). In all cases, specific threats were the focus. In contrast, most hypersexual-related psychiatric illnesses were more frequent in men than women. Thus, evidence supported the idea that extreme forms of disgust were experienced by more females than males.

6.8. Threat-induced conditions

Given evidence that females reacted more self-protectively than males to threats, it would be expected that conditions having well-established associations with threat should develop in more females than males. We therefore searched for conditions in which identifiable threats constituted clear precipitating factors, to test whether more females than males developed these conditions. We found two conditions known to be caused by stress: post-traumatic stress disorder (PTSD) and chronic fatigue syndrome also known as myalgic encephalomyelitis (CFS/ME).

Both PTSD and CFS/ME demonstrate a female preponderance. PTSD follows trauma and consists of intense, long-lasting emotional and physical symptoms, typically flashbacks, hypervigilance, and nightmares, as well as major depression, anxiety, and sleep disorders. In a WHO WMHS study in 15 diverse societies ($n > 72{,}900$), females experienced PTSD more than males (OR = 2.6) (Seedat et al., 2009).

Sex differences in experience of PTSD however must control for the nature of the precipitating stimulus. A detailed meta-analysis (290 studies) of types of trauma producing PTSD in primarily WEIRD societies showed that for every type of trauma except childhood sexual abuse, more females than males developed PTSD (OR = 1.98) (Tolin & Foa, 2006). Further detail came from a Nordic study ($n > 5{,}200$) in which approximately twice as many women (25.6%) as men (13.2%) were categorized as having PTSD (Ditlevsen & Elklit, 2012). Using a continuous measure of PTSD, females experienced stronger PTSD than males with effect sizes varying from small to large based on type of trauma: disasters and accidents ($d = 0.84$), loss ($d = 0.47$), non-malignant disease ($d = 0.47$), chronic disease ($d = 0.39$), violence ($d = 0.27$), and overall ($d = 0.60$).

While the female preponderance of PTSD could be due to more females than males experiencing severe trauma, current evidence disputed this. In the meta-analysis in WEIRD countries, fewer females than males confronted severe traumas (OR = 0.77) (Tolin & Foa, 2006). Likewise, globally, females were less likely than males to die from fatal injuries (WHO, 2014a) or become disabled due to injuries (Haagsma et al., 2016).

CFS/ME is a debilitating, often life-long condition. Along with extreme exhaustion and weakness, the most common symptoms include immune activation (flu-like symptoms), intense pain (often migraines), severe sleep disturbance, depression or anxiety, concentration problems, and adverse reactions to chemicals (Chu, Valencia, Garvert, & Montoya, 2019; Friedman, 2019; Natelson, 2019). Based on a review of 13 Asian, Australian, North and South American studies, despite varying national prevalence rates, after puberty women were 3–4 times more likely than men to develop CFS/ME (Son, 2012) with a large effect size in an American study (OR = 4.51) (Reyes et al., 2003). Onset typically occurred between ages 20 and 45 years following a specific threat: an infective illness (64% of cases), a major aversive life event (emotional stressor in the family or at work in 39% of cases), and a reaction to environmental toxins such as vaccines (20% of cases), with multiple precipitating stressors for some individuals. CFS/ME is not believed to be a disease in the typical sense, but rather a systemic reaction to stress (Cortes Rivera, Mastronardi, Silva-Aldana, Arcos-Burgos, & Lidbury, 2019). Prevalence rates of both PTSD and CFS/ME thus supported the prediction that more females than males exhibited extreme self-protective reactions to threats.

In conclusion, eight types of threat-related clinical condition, although maladaptive, may reasonably be interpreted as extreme self-protective reactions, and were more prevalent in females than males.

7. Discussion

7.1. Sex differences in self-protective responses

Our goal was to evaluate whether Campbell's (1999) SAT applied not merely to physical aggression but more generally to all threats. By searching the literature for cross-cultural evidence with large samples, we tested the hypothesis that females demonstrate more self-protective reactions than males to major threats. We found that females exhibited stronger self-protective reactions than males to important biological and social threats; a personality style more geared to threats; stronger emotional responses to threat; and more threat-related clinical conditions suggestive of heightened self-protectiveness. That females expressed more effective mechanisms for self-protection is consistent with females' lower mortality and greater investment in childcare compared with males. Table 2 summarizes our major findings. As our hypothesis would predict, the magnitudes of sex differences in self-protective reactions were largest for the most potent threats to life – including heightened antibody production, reduced endurance of pain, and greater avoidance of direct competition, with fear, disgust, and crying sometimes also producing large effect sizes.

Our test of Campbell's extended SAT is limited by our inability to examine every conceivable kind of threat, and by the incomplete availability of cross-cultural data. Nevertheless, we found evidence from many large samples and diverse cultures. Strikingly, despite intense searching, we failed to find large studies or meta-analyses that showed sex differences in the opposite direction to those expected from SAT. We conclude that the tendency for females to show more self-protective physiology, social interactions, personality styles, emotional reactions, and threat-related clinical conditions than males provides a strong first test for the extension of Campbell's SAT.

Many additional potential examples of greater female self-protectiveness occur in important areas that we excluded due to limited cross-cultural evidence. As examples, females more than males exhibit a lower threshold for detecting many sensory stimuli (Velle, 1987); remain closer to home (Ecuyer-Dab & Robert, 2004); overestimate the speed of incoming stimuli, discuss threats and vulnerabilities more frequently, find punishment more aversive, demonstrate higher effortful control, and experience deeper

Table 2 Threats, self-protective responses, extreme protective reactions, and fatal conditions with estimates of adult female:male odds ratios (OR)*.

Threat	Protective response	Extreme protective reaction	Fatal conditions overall mortality (0.66)[I]
External pathogens and internal pathologies	Antibody production (4.17)[a]	Autoimmune disease (2.46)[aa]	CVD (0.70)[II] Cancer (0.45–0.68)[III] COVID-19 (1.59)[IV]
	Non-pharmacological (1.49)[b] and pharmacological (0.89)[b] Preventive behaviors to pandemics		
Bodily damage	Adverse reactions to pictured environmental threats (1.92–4.27)[c] Lower threshold for pain (2.52)[d] Shorter endurance of pain (8.35)[d]	Migraine (2.15)[bb] Fibromyalgia (3.09)[cc]	Accidental injuries[V] Road traffic (0.37) Drowning (0.43) Poisoning (0.57) Fire-related (0.95)
Nighttime threats	Sleep disturbances (1.06–1.46)[e] Nightmares (0.94–1.60)[f]	Insomnia disorders (RR = 1.41)[dd] Nightmare disorder (2.10)[ee] Restless leg syndrome (1.63–2.22)[ff]	Obstructive sleep apnea[VI] (0.27–0.43)
Reduction of social threats and facilitation of social bonds	Smiling (2.10)[g] Politeness (1.52)[h] Emotion identification (1.36–2.67)[i] Direct competition (0.19–0.46)[j] Direct aggression (0.34–0.58)[k]	Separation anxiety disorder (1.60)[gg] Major depression (1.95)[hh] Suicide attempt (1.29–1.96)[ii]	Suicide (0.52)[V] Victim of homicide (0.23)[V]
Personality style	Neuroticism (2.07)[l]		
Emotional reactions	Fear (1.04–8.20)[m] Disgust (1.24–16.33)[n] Sadness (1.34–1.66)[o] Crying (2.26–7.45)[p] Anger (1.08)[q]	PTSD (2.60)[gg] CFS/ME (4.51)[jj] Anxiety disorder (1.70)[gg]	

*Odds ratios >1 indicate higher prevalence in females than males and <1 indicate higher prevalence in males than females.

[a] Yang and Kozloski (2011) antibodies; [b] Moran and Del Valle (2016) pandemic prevention; [c] Bradley et al. (2001), Gong et al. (2018), Gomez et al. (2013), Lang and Bradley (2007), McManis et al. (2001) adverse reactions to photographs of environmental threat; [d] Riley et al. (1998) pain; [e] Wang et al. (2019) sleep disturbances; [f] Schredl and Reinhard (2011) Hedge's *g* nightmares; [g] LaFrance et al. (2003) smiling; [h] Leaper and Robnett (2011) politeness; [i] Connolly et al. (2019), Hall (1978), Hall et al. (2000), Sasson et al. (2010), Thompson and Voyer (2014) emotion identification; [j] Klege et al. (2021), Deaner and Smith (2013) direct competition; [k] Archer (2019) direct aggression; [l] Kajonius and Johnson (2018), Schmitt et al. (2008) neuroticism; [m] Archer (2019), Arrindell et al. (2004), Brebner (200) fear; [n] Al-Shawaf et al. (2018), Atari et al. (2020), Curtis and de Barra (2018), Egolf et al. (2019) disgust; [o] Brebner (2003), Lucas and Gohm (2000) sadness; [p] Sharman et al. (2019), Van Hemert et al. (2011) crying; [q] Archer (2004) anger.

[aa] Hayter and Cook (2012) autoimmune disorder; [bb] Stovner et al. (2018) migraine; [cc] Queiroz (2013) fibromyalgia [dd] Zhang and Wing (2006) risk ratio insomnia disorder; [ee] Li et al. (2010) Hong Kong ⩾3 nightmares/week; [ff] Ohayon and Roth (2002) restless leg syndrome; [gg] Seedat et al. (2009) separation anxiety disorder, PTSD, anxiety disorder; [hh] Salk et al. (2017) major depression; [ii] Nock et al. (2008) non-fatal self-injury; Miranda-Mendizabal et al. (2019); [jj] Reyes et al. (2003) CFS in the USA.

[I] GBD (2018) mortality; [II] Mosca et al. (2011) cardiovascular disease; [III] WHO (2021) cancer mortality; [IV] Williamson et al. (2020); [V] WHO (2014a) for deaths from injuries, suicides, and homicides (we calculated ORs based on graph). We assume being a victim of homicide can be avoided to some extent through self-protective reactions. [VI] Lévy et al. (2015) obstructive sleep apnea.

empathy (Archer, 2019); express greater concern over friend's (Hall, 2011) and romantic partner's (Carpenter, 2012) loyalty; and seek more frequent help (Möller-Leimkühler, 2002; Tamres, Janicki, & Helgeson, 2002; Whiting & Whiting, 1975).

Developmental evidence generally supported the prediction that females would exhibit greater self-protective reactions than males throughout life, but that the magnitude of the sex difference would increase following puberty when females can reproduce. Sex differences in immune functioning, pain, and nighttime awakenings appeared in childhood, but increased post-pubertally. Sex differences in politeness, emotional identification, and avoidance of confrontations emerged by early childhood, but in smiling only after puberty. Sex differences in neuroticism arose only after puberty, but girls displayed some components of neuroticism more than boys pre-pubertally. Girls experienced greater fear and disgust than boys pre-pubertally, but not sadness, for which the sex difference only clearly arose post-pubertally.

We did not systematically examine sex differences in children's clinical conditions due to lack of cross-cultural evidence. However, sex differences in some conditions, such as anxiety (Rescorla et al., 2007) and depression (Salk et al., 2017), emerge only after puberty, whereas in others, such as immune functioning, shifts occur from childhood to puberty (Klein & Flanagan, 2016).

7.2. Complexities in interpreting sex differences

That numerous sex differences conform to SAT is consistent with the thesis that self-protective reactions constitute a series of evolved female adaptations. If sex differences are to be fully understood however, additional factors must be included.

First, sex/gender is a multidimensional construct resulting from the continuing interplay between biological and environmental factors (Berenbaum & Beltz, 2021; Eliot, 2009; Fausto-Sterling, 2019; Hyde et al., 2019). Further, some of its important components and related constructs, including epigenetic configurations, hormonal balances, reproductive capacity, gender identity, gender roles, and sexuality, often fluctuate over the lifespan. Thus, menarche and menopause typically produce diverse changes for human females. Males too undergo transitions. Testosterone diminishes in bachelors who marry and even further after they father children (Gettler, McDade, Feranil, & Kuzawa, 2011; Gray, Kahlenberg, Barrett, Lipson, & Ellison, 2002). Because the studies we found do not define sex/gender and treat it as binary, we cannot specify which characteristics of sex/gender relate to self-protection. More precise structural, epigenetic, cellular, hormonal, cultural, social, emotional, cognitive, and behavioral indices will greatly improve understanding of the relation between self-protection and sex/gender.

Second, the magnitude of sex differences in self-protectiveness depends on local threats and safeguards which may differentially affect females and males. For example, in matrilineal societies where females receive greater protection from kin (Smuts, 1992), girls and women appear to be as directly competitive as their male counterparts in economic games (Klege et al., 2021). Likewise, when women's rights are protected by laws, the normally higher rates of men physically battering their female partners (WHO, 2014a) can disappear (Archer, 2006). In impoverished societies that provide infants with both nutritional supplementation and breastmilk, females' immune systems are strengthened more than males' (Khulan et al., 2012; Osrin et al., 2005). Prevalence of physical illness itself varies depending on gender identity, role, and status (Mauvais-Jarvis et al., 2020) and societal kinship structure (Reynolds et al., 2020). Even sex differences in mortality are influenced by societal factors, including patients', physicians', and researchers' belief systems (Mauvais-Jarvis et al., 2020); rates of female infanticide, sexual abuse of and violence against women (Solotaroff & Pande, 2014; WHO, 2014a); and men's willingness to seek help (Verbrugge, 1989).

More individual factors also likely regulate the magnitude of sex differences in self-protective reactions. For example, grandmothers typically invest more in daughters' than sons' young children, thereby tending to maximize their own fitness (Sear & Mace, 2008). The extent of a particular grandmother's investment, however, should regulate her daughter's self-protective reactions. Similarly, although worldwide mothers care for infants (Wood & Eagly, 2002), a particular family's norms regarding the exclusivity of maternal responsibility for childcare likely influences maternal self-protective reactions. As another example, females may have lower thresholds than males to even perceive physical symptoms, social conflicts, or other threats, as extrapolation from research on pain would suggest (Riley et al., 1998). Nevertheless, the degree to which members of an individual's social network reward or punish females' versus males' expressions of vulnerability should regulate sex differences in even recognizing threats (Jansz, 2000).

Third, more research is necessary to understand the societal impact of gender equality, measured by women's participation and power in public life, on self-protectiveness. Greater gender equality is associated with even fewer women than men committing suicide (Alothman & Fogarty, 2020); and increased proportions of women than men expressing concerns about environmental degradation (Chan et al., 2019), reporting neuroticism (Costa et al., 2001; Schmitt et al., 2008), and experiencing depression (Salk et al., 2017). These somewhat paradoxical findings require further inquiry. Gender equality however is intertwined with other ecological and cultural variables (Kaiser, 2019) and may not adequately capture the realities of life of people in non-WEIRD societies (Markus, 2021).

Fourth, a large overlap exists between the sexes in many self-protective reactions as is found in many studies of sex differences (Eliot, 2009; Hyde et al., 2019; Zell et al., 2015). Consequently, a particular self-protective response cannot be predicted simply from knowing an individual's binary sex. Our evidence merely demonstrates that there is a population-wide tendency in the direction predicted by Campbell's theory.

Distinct self-protective responses, however, frequently co-occur. Myriad studies report links among somatic, social, neurotic, emotional, and clinical responses (Okur Güney, Sattel, Witthöft, & Henningsen, 2019; Yunus, 2007). This suggests that aggregating self-protective reactions could more accurately describe the effect of greater self-protectiveness on females' than males' lives than simply comparing the sexes on only one self-protective response at a time. Thus, multivariate statistical techniques could provide a more qualitative distinction between the sexes (Del Giudice, 2022).

Fifth, many female-prevalent illnesses and clinical conditions could impede women's ability to care for their children, thereby reducing their fitness. An adaptive approach however suggests that the benefits accrued from women's greater longevity outweigh the costs of chronic illness (Del Giudice, 2018; Nesse, 2005).

Overall, considering the diversity of our evidence, the consistency of our findings is striking. Accordingly, we regard sex differences in self-protective responses as important to investigate not only for theoretical reasons but also for practical value related to medical and psychological health (Clayton, 2016; Shansky & Murphy, 2021).

An analysis of rates of COVID-19 illustrates how sex differences can vary widely in magnitude without undermining their significance. Both absolute frequencies and sex differences vary markedly by ethnicity, age, geographical location, socioeconomic status, and baseline health status even within the same country, as depicted in Figure 9 for England (Economist, 2020).

Despite this variation, women are almost always less likely than men to die within each demographic group. Thus, sex constitutes an important biological variable that can enhance causal understanding of a phenomenon which varies on many factors (Clayton, 2018).

Finally, further research is necessary to understand whether some threats elicit stronger self-protective reactions in men than women. Examples include male concerns over status and warfare. Current evidence however indicates no sex differences in the desire to attain status (Anderson, Hildreth, & Howland, 2015), even though the sexes may choose different strategies to achieve it (Benenson & Abadzi, 2020). Whether men are more concerned than women about imminent military attacks has not been investigated.

7.3. Complementary explanations

Our findings provide support for self-protective responses as a female adaptation. Alternative, but potentially compatible, explanations however could also apply.

First, males' higher levels of androgens, larger body size, more negative social interactions, greater risk-taking, and other sexually selected characteristics related to mate competition are expected to partially explain why males exhibit lower self-protectiveness than females (Dunsworth, 2020; Klein, 2000; Kruger & Nesse, 2006; Zuk, 2009). Individual and population variation among males in their optimal strategies and biological constraints will therefore contribute to explaining their lower self-protectiveness. Nevertheless, it is not simply degree of mate competition that produces sex differences in self-protectiveness. Rather, females invest in costly self-protective mechanisms, including immune

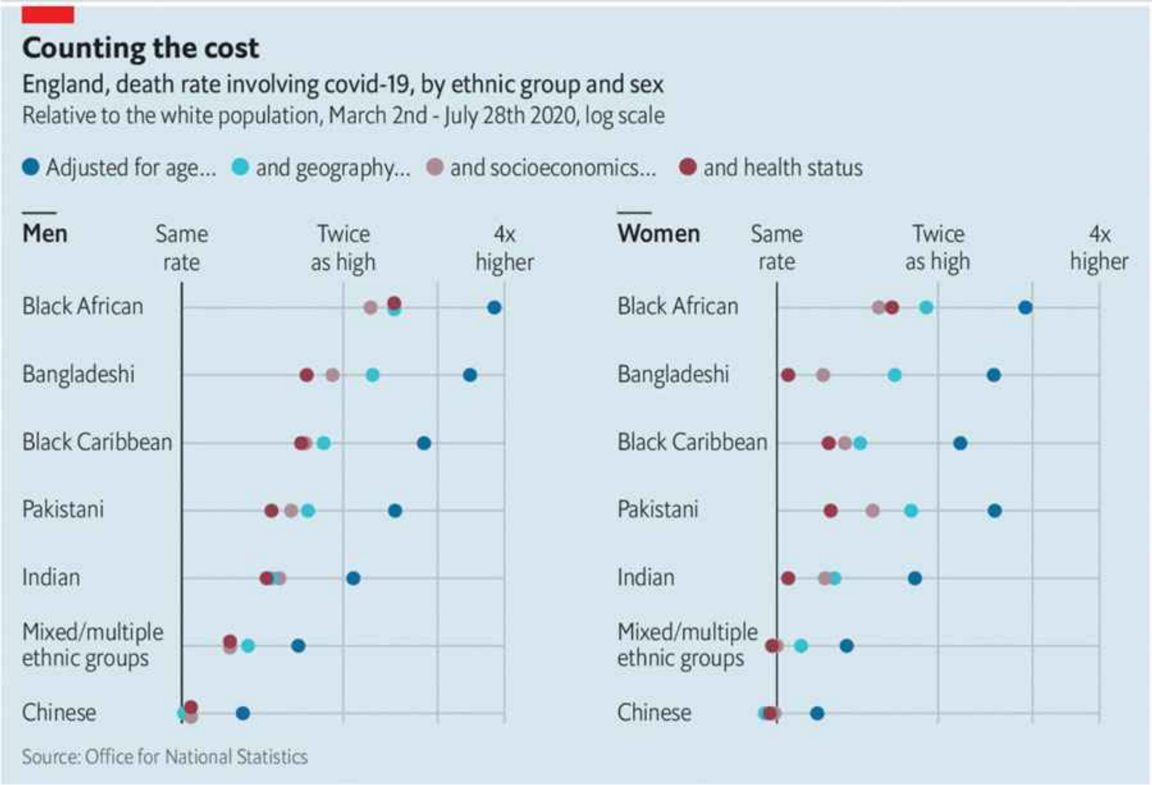

Figure 9. Sex differences in frequency of COVID-19 infections across varied demographic factors in England. © The Economist Group Limited, London (November 21, 2020).

functioning and conflict reduction measures, that elevate the probability of survival. Independent selective pressures on both male and female traits influence the nature and degree of sex differences in self-protectiveness.

Unquestionably, women's smaller size and muscle mass enhances their self-protectiveness with men. Nonetheless, sex differences in size and strength alone cannot explain all self-protective reactions. For example, in children where sex differences in size and muscularity are minimal, girls often exhibit more self-protective reactions than boys, including greater pain to vaccines (Chambers et al., 1999) or politer language (Leaper & Smith, 2004; Whiting et al., 1988).

Second, a "trauma hypothesis" might suggest that traumas specific to women increase their self-protectiveness. Worldwide, one in three women suffers domestic or sexual violence; 20% of girls are sexually abused; and reproductive-related morbidity and mortality are more frequent where women have fewer rights (WHO, 2014a). However, universally more men than women are exposed to lethal threats (WHO, 2014a). If trauma alone were responsible for greater self-protectiveness, then men should exhibit stronger self-protective responses than women in some areas, such as in response to violent social interactions or accidents which affect men more (WHO, 2014a), but they do not (Ditlevsen & Elklit, 2012). Many of the sex differences we reviewed therefore are not explicable by the trauma hypothesis.

Third, women's greater self-protectiveness could result from the high costs of pregnancy and lactation which could render women less physically, socially, emotionally, and clinically functional than men. This view is commonly held by medical and psychological professionals who perceive "self-protective" reactions as maladaptive or compensatory (Chesler, 1972; Cleghorn, 2021). If reproduction itself were the only critical factor however, sex differences in self-protective reactions would be highest during pregnancy and lactation, but this is not the case. Some sex differences in self-protectiveness appear by infancy (e.g., immune functioning, fear); others arise at puberty (e.g., smiling, sadness); some are maximal throughout the reproductive years (e.g., neuroticism, migraine); and others increase with age (e.g., insomnia).

Fourth, worldwide men tend to hold higher status than women, particularly in the public sphere (Fiske, Dupree, Nicolas, & Swencionis, 2016; Rosaldo & Lamphere, 1974). This difference almost certainly heightens females' self-protective reactions compared to when females hold power such as within the confines of families or in matrilineal societies (Smuts, 1992). Status differences do not readily explain other socially self-protective reactions, however, such as females' greater fearfulness (Else-Quest et al., 2006) or more accurate emotional identification (McClure, 2000) from infancy onwards.

In sum, the evolutionary explanation offered by SAT complements other accounts of women's greater responses to threats by integrating divergent domains. Further, it views females' strategies as evolved adaptive functions, rather than being constrained features that are sub-optimal compared to those of males. It also helps resolve many apparent paradoxes in which women are *less* likely than men to die from pathogens, injuries, social conflicts, and suicide, yet *more* likely to experience physical symptoms, pain, sleep disturbances, avoidance of social conflicts, generalized worry, fear, disgust, and sadness, and make suicide attempts. SAT posits that stronger self-protective reactions to threat enhance survival, rendering females less vulnerable than males. Furthermore, SAT would predict that individuals who assume primary responsibility for children's well-being will increase their self-protective reactions so as to enhance their own survival.

7.4. Conclusion

Girls' and women's heightened responsiveness to physical and social threats, neuroticism, emotional reactions to threats, and related clinical conditions are often pathologized, that is, attributed to hysteria, mental health disorders, or other abnormalities, because men are the reference point (Chesler, 1972; Cleghorn, 2021). Our extension of Campbell's SAT suggests, by contrast, that females' "sensitivity" should be construed not as a constrained weakness or compromise enforced by reproductive biology but as a strategic approach to counteracting threats. Male traits, equivalently, that are often seen as the norm, are suboptimal for enhancing survival, but serve to maximize men's fitness given the constraints that they confront (Seager, 2019). Thus, independent consideration of each sex, along separate dimensions, is necessary for understanding the ways in which each sex's traits are optimized. Had the evidence existed, we would have compared the reproductive success of females who varied in their degree of reactions to threats, and not included males at all.

A richer understanding of the adaptive nature of female self-protection ultimately will depend on discovering its underlying mechanisms and how they may have co-evolved. Promising mechanisms undergirding self-protectiveness include sex chromosomes (Schurz et al., 2019), sex hormones (Klein & Flanagan, 2016), centralized reactivity (Yunus, 2007), support of attachment figures (Archer, 2008; Bowlby, 1980) and the larger community (Smuts, 1992), and degree of responsibility for offspring survival (Allman et al., 1998).

In conclusion, in response to a wide diversity of threats, human females exhibit greater self-protective responses than males. This finding suggests an opportunity for researchers and clinicians to better understand the adaptive nature of diverse female traits, both in humans and other species.

Acknowledgements. The authors sincerely thank Dr. Barbara Finlay and the six reviewers for their excellent recommendations which greatly improved the manuscript.

Funding statement. This research received no specific grant from any funding agency, commercial or not-for-profit sectors.

Conflict of interest. None.

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Open Peer Commentary

Beyond individual sex differences: "Staying alive theory" as an adaptive complex

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doi:10.1017/S0140525X22000577, e129

Abstract

Extended staying alive theory (SAT) raises the issue of the extent to which its various attributes are linked or whether they provide alternative means to the same adaptive ends. Theories such as SAT that consider an array of sex differences may benefit from the application of the multivariate *D* statistic, rather than using a series of *d* values, as is common at present.

Most contemporary evolutionary explanations of sex differences in aggression involve inter-male competition, a component of sexual selection (Darwin, 1871/1901; Trivers, 1972). Campbell (1999) departed from this by examining selection pressures on females, proposing that sex differences in aggression and associated attributes arose from selection pressures on females to facilitate staying alive, and consequently being more likely to rear their offspring to maturity. The target article widened Campbell's "staying alive theory" (SAT) to include a range of self-protective reactions to various kinds of threat. Extended SAT provides a new way of considering attributes that are at present viewed individually (often as pathologies), enabling them to be viewed as a set of female adaptations.

The extended SAT raises the question of whether the specific attributes covered, such as immune responses, pain thresholds, emotions, and personality, form a coherent adaptive complex, and if so whether they are linked to one another at an individual level, so that someone with a strong immune response also shows a low pain threshold and more sleep disturbances. Alternatively, the various attributes covered by SAT may represent alternative ways of achieving the adaptive end-result of facilitating female longevity.

In psychology, discussions and syntheses of psychological sex differences have typically focused on individual attributes rather than coherent groups of attributes. This follows earlier syntheses rooted in individual differences research (e.g., Garai & Scheinfeld, 1968; Maccoby & Jacklin, 1974), culminating in more recent times with meta-analyses of specific attributes. These meta-analyses were synthesized by Hyde (2005) and Zell, Krizan, and Teeter (2015), both presenting sex differences as a list and calculating the percentage that were of different magnitudes (large, medium, small, or null). Conclusions were drawn on the basis of how many of these attributes fell into the different categories. Links between the individual attributes were not part of this approach, which is essentially atheoretical.

In contrast, broad theoretical explanations, whether they be in terms of social roles (e.g., Eagly, 1987; Wood & Eagly, 2012) or evolutionarily based adaptive complexes, such as sexual selection (Archer, 2019), or the extended SAT, raise the issue of how the various attributes might be related to one another. The statistical underpinning of sex differences viewed as sets of attributes, rather than individual items, has only recently begun, following the work of Del Giudice (2009). For example, from an evolutionary perspective, sex differences in aggression can be viewed as being linked to other attributes that are the evolutionary consequence of male competition, such as bodily strength (Sell, Eisner, & Ribeaud, 2016; Sell et al., 2009). Likewise, the attributes considered in the revised SAT could be regarded as an adaptive complex or as a series of alternative adaptations whose common function is to minimize mortality in the sex that is the primary caretaker of the offspring.

The meta-analyses and large-sample studies that form the bases of existing syntheses of studies of sex differences are usually concerned with specific attributes, such as aggression, or depression, and typically the summary statistic used is Cohen's *d*, the standardized difference between the mean values for males and for females. This is appropriate for summaries where attributes are viewed as independent items (e.g., Hyde, 2005; Zell et al., 2015). However, where groups of coherent attributes are being considered, it may be appropriate to consider such groupings together and to apply the multivariate *D* statistic (*Mahalanobis* distance), which represents the distance between the two sexes in multivariate space. Despite some persuasive arguments that this type of analysis is the appropriate way forward (e.g., Del Giudice, 2009; Del Giudice, Booth, & Irwing, 2012; Eagly & Revelle, in press), it has seldom been carried out in practice (for exceptions, see Lippa [2001], for masculinity–femininity; Conroy-Beam, Buss, Pham, & Shackelford [2015], for mate-choice criteria).

Both the modified SAT theory, and my own evolutionarily based review of sex differences (Archer, 2019), relied on the more conservative approach of using *d* vales as summaries of sex differences in individual attributes. This underestimates the size of differences, so that when these are considered as groups of attributes using the multivariate Mahalanobis *D* (Eagly &

Revelle, in press), much larger values are typically found than when individual d values are averaged: One important caveat is that larger Mahalanobis D values are obtained where the individual attributes show lower intercorrelations. These observations lead back to the empirical question of the extent to which individual attributes covered by SAT form a coherent grouping, or represent alternative responses that all have the consequence of reducing mortality.

A final point is the extent to which the extended SAT complements or replaces sexual selection as an evolutionary explanation of human sex differences. In view of coherent sets of male attributes (musculature, aggression, impulsiveness), it is likely to be complementary, although this could be subject of future study. To begin with, it would be a simple matter to compare the scope of the present article to the attributes associated with sexual selection in previous syntheses (e.g., Archer, 2019; Daly & Wilson, 1988), and the extent to which these two groupings were related or independent. The extended SAT could also be applied to relevant within-sex variations: We would predict that men showing greater degrees of paternal care would score higher on attributes covered by the modified SAT.

Financial support. This research received no specific grant from any funding agency, commercial, or not-for-profit sectors.

Conflict of interest. None.

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Sex differences are insufficient evidence of ecological adaptations in human females

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doi:10.1017/S0140525X22000541, e130

Abstract

Benenson et al. postulate that human females evolved unique survival adaptations to facilitate maternal and grandmaternal care. This hypothesis is consistent with the broader hypothesis that female phenotypes are more ecologically optimal, but further evidence is needed to make a compelling case that sex differences in self-protection are not primarily the result of more intense sexual selection on males.

Benenson, Webb, and Wrangham note that sexual selection explains many traits of human males and suggest that "no unifying theory explains traits expressed more in females." They therefore propose a generalized version of Campbell's "staying alive" hypothesis: Human females evolved unique, self-protective survival adaptations driven by the importance of maternal and grandmaternal care. Benenson et al. review evidence in support of this hypothesis, including evidence that females live longer and show less risk-taking behaviors, greater avoidance of interpersonal conflicts, lower pain thresholds, more effective immune responses, and more frequent sleep disturbances.

We agree that theory and data suggest that human females exhibit stronger self-protective reactions than males do, and that these reactions were likely adaptive for ancestral females. These ideas indeed help unify our understanding of some female adaptations – though not others, such as fat deposition on the breasts, hips, and buttocks, which are putative sexually selected female ornaments that may be costly to survival (Pawłowski & Żelaźniewicz, 2021), and maternal investment through gestation and lactation, which deplete energy reserves and decrease longevity (Wood, 2017). Here, we make two additional points to advance this discussion.

First, there is a more general theory that links a broader set of human female traits: Females are the more "ecological sex" (Gaulin & Sailer, 1985). While sexual selection favors traits that aid in mating competition, ecological selection favors traits for other functions, including survival, fecundity, and offspring survival. Gaulin and Sailer (1985) provided evidence that nutritional factors influence the evolution of primate body size, but males deviate further from the ecologically optimum size in species in which they compete more intensely for mates. Gaulin and Sailer (1985) note that the hypothesis that females tend to be more ecologically optimized "is a very general one. The idea that the precision of ecological adaptation will vary with both sex and mating system suggests a functional perspective from which any morphological, physiological, or behavioral pattern of sex differences might be studied" (p. 117). The hypothesis that females, more than males, possess self-protective adaptations thus accords well with the more general hypothesis that females are relatively optimized under ecological selection compared to males in species in which males experience stronger sexual selection.

Second, more evidence is needed to make a strong case that specialized survival adaptations evolved in human females. Such adaptations may instead have been selected in both sexes, with a lower level of expression favored in males due to tradeoffs with traits favored in mating competition, and many survival adaptations are likely to be ancestral and not human specializations. Benenson et al. state that "it is not simply degree of mate competition that produces sex differences in self-protectiveness," but the problem with inferring otherwise from the evidence reviewed by Benenson et al. is that this evidence consists of human sex differences in various traits, and sex differences can result from adaptations in either sex. Without additional evidence, a sex difference in the degree of mating competition remains the more parsimonious explanation.

For example, Benenson et al. claim that greater female longevity is an evolutionary response to women's larger role in childcare, but cross-species data are needed to pull apart contributions of female parental investment from male sexual selection. In all mammals, females engage in greater parental investment, but males outlive females in approximately 40% of wild mammal populations (Lemaître et al., 2020). Sex differences in longevity appear to relate more consistently with the intensity of sexual selection in males (Tidière et al., 2015), which may lead to male phenotypes that are more susceptible to environmental threats (Lemaître et al., 2020). Human sex differences in mortality due to homicide, suicide, and accidents are also highest in young adulthood when male mating competition is most vigorous (Wilson & Daly, 1985).

Reduced female risk-taking and same-sex aggression are shared with humans' close living relatives (Harrison, Noble, & Jennions, 2021; Rohner, 1976), and sex differences in these traits were likely present in the common ancestor of the great apes because risk-taking and aggression increased male mating success and the expense of survival (Archer, 2009; Carter & Kushnick, 2018; Flinn, Ponzi, & Muehlenbein, 2012; Kruger, Wang, & Wilke, 2007; Luoto & Varella, 2021; Muñoz-Reyes et al., 2020; Puts, Carrier, & Rogers, in press). Decreased responses to pain and decreased pain sensitivity in males may also reflect an evolutionary history of male–male mating competition (Archer, 2019; Puts et al., in press; Vigil et al., 2013), and susceptibility to infectious disease may be a costly side-effect of the development of sexually selected male traits (Folstad & Karter, 1992; Moore & Wilson, 2002).

Benenson et al. propose that sex differences in nighttime awakenings and disturbances reflect heightened vigilance to physical and social threats among women. However, mating competition has also likely shaped patterns of sleep sacrifice (Faria, Varela, & Gardner, 2019), and when sleep sacrifice is used to protect the group against threats during nighttime, evolutionary theoretical models predict that females should sleep more, not less, than men (Faria et al., 2019). Some evidence indicates that women sleep longer than men (Burgard & Ailshire, 2013) and have better sleep quality (Faria et al., 2019). In BaYaka foragers (Kilius et al., 2021), males displayed a higher variance in sleep patterns and spent more time socializing during nighttime.

Relatively stronger ecological selection may indeed have shaped specialized survival adaptations in human females (Campbell, 2010; Stockley & Campbell, 2013), but further evidence is needed to make a compelling case. Are these putative survival adaptations more prevalent in primate species in which females invest more in offspring, controlling for levels of male mating competition? Are some unique to human females? Many traits in human males, such as muscularity, low voice pitch, and facial hair, emerge at puberty when male mating competition intensifies (Aung & Puts, 2020; Puts, 2016). Do some putative female survival adaptations emerge across pregnancy or parturition, after female mating competition becomes less exigent in relation to the importance of surviving to care for offspring? We look forward to learning more.

Conflict of interest. None.

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Societies also prioritize female survival

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doi:10.1017/S0140525X22000528, e131

Abstract

We extend Benenson et al.'s hypothesis from the individual level to the societal level. Because women have highly limited reproductive rates, societies have generally prioritized female survival and regarded males as expendable. We describe various lines of evidence that are consistent with this hypothesis, and we offer additional predictions about differential attitudes toward male versus female endangerment.

In support of the general proposal that staying alive has historically been more important for females' reproductive success than for males' (Campbell, 1999), Benenson et al. provide extensive evidence that females respond to a variety of threats with greater self-protectiveness than do males. We propose that the logic of Benenson et al.'s analysis extends to the societal level. In particular, because women, but not men, set the upper limit on reproduction, societies have generally prioritized female survival and protection from harm.

We suggest that societies prioritize women because groups with few men and many women produce more offspring, and ultimately achieve greater success, than groups with few women and many men (Baumeister, 2010; Felson, 2000). This idea is supported by historical and ethnographic data from both hunter gatherers and large-scale societies (Glowacki, Wilson, & Wrangham, 2020). A prioritization of female survival predicts the existence of individual thought and behavioral patterns, as well as group-wide norms, that promote the survival of women over men. We note that the prioritization of female survival does not imply a prioritization of female autonomy and sexual choice.

Much evidence supports the hypothesis that societies prioritize female survival. First, people's self-reported attitudes reflect more concern about preserving women's survival than men's. For example, when asked who should be saved first on a sinking ship, people are far more likely to say women than men (FeldmanHall et al., 2016; see also Burnstein, Crandall, & Kitayama, 1994). This attitude manifested on the sinking *Titanic*, where men prioritized the survival of women and children above their own, so much so that men traveling first class were more likely to perish than were women traveling third class (80% of men perished in all, compared to 25% of women; Browne, 2007). This behavior has been observed on other sinking ships, and the norm is indicated by written statutes and captains' orders; in cases where men failed to prioritize women and children, they were publicly shamed (Browne, 2007).

Warfare and military norms and attitudes prioritize female survival. Worldwide, warfare has been pursued almost exclusively by groups of men against other groups of men (Chagnon, 1988; Keeley, 1996). Historically, women have been barred from military combat positions (in the United States, women were banned from direct ground combat military positions until 2013), and in rare cases where industrialized states have used women in combat, it has been done as a last resort (Browne, 2007). The exclusion of women from combat reflects, at least in part, concerns about their survival: Female combat casualties cause greater societal despair than male casualties; and male soldiers reported that if women were in their combat units, they would feel more protective of them than of their male comrades (Browne, 2007).

The workforce reveals trends consistent with a prioritization of women's survival. In the United States, men are massively overrepresented in the most dangerous jobs and they represent over 90% of occupational fatalities (Bureau of Labor Statistics, 2020, 2022). When emergencies pose grave risks to workers (e.g., Fukushima, Chernobyl), nearly all of the rescue workers are men (ABC News, n.d.; Belyakov, Steinhäusler, & Trott, 2000).

Physically dangerous sports also do not generally include women (Deaner & Smith, 2013). Although this may be due to both informal social norms and sex differences in risk-taking, formal policies exist: In both ice hockey and lacrosse, men but not women are permitted to initiate physical contact against (i.e., check) their opponents.

Cognitive biases in perceptions of women are also consistent with a prioritization of female survival. Males and females alike are more likely to automatically categorize a "victim" as female rather than male, to perceive the same offense as causing more harm to females than to males, and to desire harsher punishment to perpetrators who target female versus male victims (Reynolds et al., 2020). Relatedly, people view an act of physical aggression perpetrated against a woman as more serious than the same act of aggression perpetrated against a man (Felson, 2000; Harris & Knight-Bohnhoff, 1996), and offenders who commit violent crimes against women receive longer sentences than do those who commit crimes against men (Curry, Lee, & Rodriguez, 2004; Glaeser & Sacerdote, 2003).

The norm of (many) societies prioritizing the survival of women could reflect cultural group selection (Richerson et al., 2016; Turchin, Currie, Turner, & Gavrilets, 2013). However, it could also reflect men protecting unrelated women and children ("chivalry") in order to signal their genetic quality, parenting ability, and general pro-sociality; this hypothesis is consistent with data from nonhuman primates (van Schaik, Bshary, Wagner, & Cunha, 2022).

One strength of the hypothesis that societies prioritize female survival is that developmental mechanisms that operate at the societal level may partly explain greater female self-protectiveness at the individual level. For example, as summarized by Benenson et al., girls and women generally experience greater fear than their male counterparts; this difference likely has several causes, but one may be societal messages that promote male, but not female, bravery, pain tolerance, and risk taking, particularly if there is an audience. These messages may be transmitted by family members, other adults, and social narratives.

The hypothesis that women's survival is prioritized generates additional predictions about attitudes toward males and females, including the following: (1) people should be more concerned about women serving in direct combat positions than about women serving in military command positions; (2) parents should be less supportive of daughters' than sons' participation in dangerous sports such as mixed martial arts and cliff-jumping; (3) men and women should be less inclined to encourage females than males to consider high-risk occupations, such as law enforcement and truck driving; and (4) the degree to which people harbor negative feelings about female participation in direct ground combat military roles and high-risk sports and occupations should be mediated by their perceptions of how physically dangerous those choices are as opposed to their perceptions of how stereotypically male-oriented or unpopular those activities are.

Financial support. This research received no specific grant from any funding agency, commercial, or not-for-profit sectors.

Conflict of interest. None.

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Sex-dependent selection, ageing, and implications for "staying alive"

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doi:10.1017/S0140525X2200053X, e132

Abstract

Incorporating theoretic insights from ageing biology could advance the "staying alive" hypothesis. Higher male extrinsic mortality can weaken selection against ageing-related diseases and self-preservation, leading to high male intrinsic mortality. This may incidentally result in female-biased longevity-promoting traits, a possibility that will require rigorous testing in order to disentangle from the adaptive self-preservation hypothesis presented in the target article.

The authors, and the originator of the "staying alive" hypothesis (Campbell, 1999), identify that sex differences in the timing of male and female contributions to fitness can result in the evolution of sex differences in survival and the mechanisms that prolong life. The hypothesis seeks to explain women's greater longevity as the result of female-specific longevity-promoting adaptations. Those adaptations are thought to have evolved because, relative to men, women have historically gained greater marginal fitness from post-partum contributions to offspring and grand-offspring fitness. This proposal complements the more commonly articulated argument that stronger selection among men to succeed in pre-copulatory sexual competition leads them to take more risks, be more violent, and thus die younger than women.

Our commentary points to some areas where "staying alive" might be more thoroughly integrated with theory and empirical research on ageing and life histories. Such integration would allow both critical testing of "staying alive" and other human-centric hypotheses and enrich the evolutionary study of sex-dependent human ageing. Many of the background references in the target article are from research on ageing, and many of the traits discussed – including cancers, dementia, cardiovascular diseases, autoimmune diseases, and age-dependent immune responses – are related to ageing. Placing "staying alive" into the theoretic context of ageing biology would constitute an important next step for the hypothesis.

Ageing research has found value in distinguishing *extrinsic* mortality due to age-independent hazards such as accidents and general predation from *intrinsic* mortality due to age-dependent decreases in performance (Kirkwood & Austad, 2000; Williams, 1957). While the distinction can often be artificial, it remains useful in thinking about the evolution of mechanisms that slow or prevent ageing, including immune and behavioural self-protection. The fact that some extrinsic mortality is unavoidable means that mechanisms of somatic repair are always going to be under weaker selection in older cohorts than in younger ones.

This distinction is important because the reasons presented for greater female lifespan in humans and in other animals are often tied to greater extrinsic mortality in males. Higher predation due to male ornamentation, accidents due to risk-taking, and male–male aggression all have the potential to weaken the selection against both diseases of ageing and self-preservation behaviours in males relative to females (Austad & Bartke, 2016; Bonduriansky, Maklakov, Zajitschek, & Brooks, 2008). High male extrinsic mortality can thus lead on to higher intrinsic mortality.

Observations across a variety of taxa suggest that such a pattern may commonly pertain (see Bonduriansky et al., 2008 for a review; Promislow & Harvey, 1990). In many taxa, males are more likely than females to "live fast and die young" due to differences in the intensity of sexual competition (Promislow, Montgomerie, & Martin, 1992). In humans, evidence suggests that young men are particularly prone to discount the future and risk their lives in the pursuit of status, wealth, and, ultimately, matings (Wilson & Daly, 1985), and that women's fitness is more likely to benefit from long-term investment in children and grandchildren (Hawkes, 2004).

Humans are, by any comparison, a long-lived species with extended contributions from mothers, fathers, and alloparents to offspring. Viewed in the context of other species, both women and men have extraordinary self-preservation and anti-ageing traits that drive very long mean and maximum lifespans. Nonetheless, sex-differences in extrinsic mortality may be responsible for sex-dependent patterns of intrinsic mortality, including many of the traits reviewed in the target article. These traits may be over-represented in women both because staying alive enhances female fitness and because higher male extrinsic mortality has weakened selection in favour of these traits among men.

The claim that women's fitness benefits more from self-preservation than men's fitness, while consistent with the majority of evidence presented in the target article, is thus an empirical claim that needs critical testing. Theoreticians and comparative biologists have pointed out that in animal species in which small numbers of males live long enough to grow large, develop large weapons, or achieve high social rank, selection may promote male lifespan and suppress male ageing more strongly than female (Clinton & Le Boeuf, 1993; Graves, 2007). In humans, the importance of social status to men's mating success may have a similar effect, and has been suggested to be at least partly responsible for the evolution of extended human lifespans (Tuljapurkar, Puleston, & Gurven, 2007).

Further, although women's life expectancy currently exceeds men's in most countries, that has not always been the case. Throughout history, extraordinary numbers of women have died in childbirth, and higher parities and costs of reproduction are, in some places and at some times, associated with men living longer than women (Bolund, Lummaa, Smith, Hanson, & Maklakov, 2016; Maklakov, 2008).

Sex-differences in lifespan, age-dependent reproduction, and thus selection are variegated, complex, and often environmentally contingent. To add further complication, changes in the timing of reproductive effort and in ageing-related traits can both precede and follow changes in survival (Austad & Bartke, 2016; Bonduriansky et al., 2008). As a result, relationships between selection on lifespan and the traits that result are often more complex and confusing than the target article concedes. This is not a criticism of a target article and the choices made under publishing constraints, but rather a call for further theoretic development and hypothesis testing.

In conclusion, the authors of the target article are to be congratulated on assembling such a varied and thorough set of published observations which, together, appear to weigh heavily in favour of the "staying alive" hypothesis. Greater integration with life history theories of ageing, and with the genomics of sex-dependent variation in fitness traits (Bonduriansky et al., 2008), together with a commitment to critically testing the adaptive intuition behind the hypothesis will likely broaden its relevance and spur a flurry of exciting research.

Financial support. The authors are supported by the Australian Research Council, grants DP220101023 and DE210100800.

Conflict of interest. No conflicting interests declared.

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Staying alive includes adaptations for catalyzing cooperation

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doi:10.1017/S0140525X22000565, e133

Abstract

The target article interprets women's lower competitiveness than men's as evidence of adaptation to help women avoid physical conflicts and stay alive. This commentary advances the additional hypothesis that strategically suppressing competitiveness, thus signaling egalitarian intentions, could be an adaptation to catalyze cooperative behavior from males and females, turning natural competitors (other women) into allies and men into supportive partners.

Benenson, Webb, and Wrangham's (2022) article interprets women's lower competitiveness compared to men's as evidence of an adaptation that would permit females to avoid physical conflicts, thereby helping them with staying alive (Campbell, 1999). Among other strategies – such as smiling, politeness, and emotion identification – avoidance of confrontations is posited as having the potential to reduce hostile interactions. Specifically, the argument focuses on the results of competitiveness experiments in which women are systematically determined less likely than men to compete against others (Klege, Visser, Barron, & Clarke, 2021; Niederle & Vesterlund, 2011; Sutter, Zoller, & Glatzle-Rutzler, 2019). It concludes that such behavior should reduce interpersonal conflicts and decrease social tensions. Recent economic evidence suggests that we could take Benenson, Webb, and Wrangham's hypothesis one step further, and venture that women not only avoid direct competition to reduce interpersonal conflicts, but also to actively pursue strategies that increase the opportunities to cooperate with others, both males (as mates or potential romantic partners) and other females (as allomaternal helpers). Such proactive prosocial strategy should be included as another behavioral pillar of staying alive theory. Some evidence in support of this hypothesis is as follows.

First, the competitiveness elicited by economics games is reminiscent of labor markets, where confrontations rarely escalate to the level of physical attacks. Individuals competing for CEO positions do not usually resort to eliminating contenders. Gaining prestige, rather than physical violence, may be a more frequent way to climb rank in the economic sphere (Cheng, Tracy, Foulsham, Kingstone, & Henrich, 2013). This suggests an alternative hypothesis for why women shy away from competitive environments: Such systematic preference could actually derive from an evolved avoidance of situations with unequal distributions of resources. Inasmuch as it produces non-egalitarian outcomes, competitions may put further cooperation between winners and losers at risk (Bartling, Fehr, Maréchal, & Schunk, 2009). Data from a wide variety of experiments indicate that women are not necessarily always more generous than men (Croson & Gneezy, 2009; Eckel & Grossman, 1998), but they do systematically prefer equal distributions of resources and power more strongly than men (Andreoni & Vesterlund, 2001; Dufwenberg & Muren, 2006; Fehr, Glätzle-Rützler, & Sutter, 2013; Selten & Ockenfels, 1998). Inequalities of resource, power, and status may erode cooperation based on reciprocity and mutual altruism, while egalitarianism could be a critical factor for the evolution of strong reciprocity and cooperation (Andreoni, Harbaugh, & Vesterlund, 2003; Boehm, 1999; Bowles, 2006; Dawes, Fowler, Johnson, McElreath, & Smirnov, 2007; Fehr, Fischbacher, & Gächter, 2002; Hooper, Kaplan, & Jaeggi, 2021). Cooperation based on reciprocity may have been especially relevant for women who, for large part of human history, had to leave their family, reside with their husbands' kin, and rely on non-kin and strangers for help (Kaplan, Hill, Lancaster, & Hurtado, 2000; Seielstad, Minch, & Cavalli-Sforza, 1998). So, rather than competitiveness *per se*, women may be particularly susceptible to non-egalitarian distributions of resources. If egalitarianism is a catalyst for sustained cooperation, as both theory and experimental evidence suggest, and cooperation based on reciprocity is more attuned to women than to men, women may actively try to protect its potential by avoiding environments that create inequalities.

Second, the lower female competitiveness reported in economic experiments is mainly observed when women compete against men or in mixed groups (e.g., Geraldes, 2020). Importantly, recent research shows emerging evidence of the costs borne by women who compete and succeed in the economic and political arenas, penalties felt both on the household front and with same-sex individuals. Women who obtain high status in society by reaching high-executive and political positions appear not to gain commensurate advantages in attracting higher quality men (Fisher, 2013; Fisman, Iyengar, Kamenica, & Simonson, 2006), are more likely to get divorced than men (Folke & Rickne, 2016), are subject to adverse reactions from their partners, and report lower marital satisfaction (Bertrand, Kamenica, & Pan, 2015). Furthermore, for women, having more status, power and resources may alienate the support from other women (Benenson, 2013; Benenson & Markovitz, 2014). Yet, the benefits to securing the continued support of resource-holding mates and the assistance of other women are far-reaching for the women's own outcomes and their offspring's (Geary, 2000; Hrdy, 2009; Rucas, 2017). Hence, strategically downplaying one's competitiveness may be a fundamental strategy – likely unconscious or the result of self-deception (Von Hippel & Trivers, 2011) – for attracting and maintaining mates, securing same-sex allies, and sustaining their cooperation.

Third, lower female competitiveness is not a universal find (for a review of this literature, see Cassar & Rigdon, 2021a). Even in cultures and samples in which a competitiveness sex gap exists, it responds to incentives and a change in the game rewards can greatly reduce it. Namely, in a first series of experiments across different cultures, substituting cash rewards with prizes that benefit the children of the participants eliminates the difference in competitiveness between mothers and fathers (Cassar, Wordofa, & Zhang, 2016; Cassar & Zhang, 2021). In a second series of experiments, adding a prosocial option (where the winners can send some of their rewards to the losers) increases women's competitiveness to the men's levels (Cassar & Rigdon, 2021a, 2021b). These findings suggest that it is not competitiveness *per se* that women lack, but, rather, that women more than men are particularly interested and responsive to the social aspects of competitions.

In conclusion, this body of evidence suggests that women may strategically downplay their competitiveness not just to reduce potentially dangerous interpersonal conflicts but, primarily, to actively elicit cooperative behavior from both males and females. In intra-sex competitions, by signaling egalitarian intentions, women may turn natural competitors into supportive allies based on reciprocity. In inter-sex competitions, the suppression of competitiveness when facing a male (whose higher competitiveness, on the contrary, may signal good male mate value) would be an adaptation for catalyzing women–male cooperation for "the formation of alliances to raise children." Staying alive requires the strategic reduction of competitiveness as an adaptation for eliciting cooperation for the benefit of offspring.

Financial support. The research of mine discussed in this article received funding from the National Science Foundation (SES#1919535) and the University of San Francisco.

Conflict of interest. None.

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Toward a more domain-specific conceptualization of female traits: A commentary on Benenson et al. (2022)

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doi:10.1017/S0140525X22000450, e134

Abstract

Benenson et al. (2022) amass impressive evidence of robust sex differences as support for expanding "staying alive" theory. We argue for a broader and more domain-specific conceptualization focusing on life history tradeoffs between survival and mating success. Using three examples – women's disgust, fear of rape, and cultivation of bodyguards – we illustrate these tradeoffs and suggest a broader theoretical framework.

Benenson, Webb, and Wrangham's (2022) expansion of "staying alive" theory (SAT; see Campbell, 1999) posits that females have evolved an array of specific adaptations as defenses against survival threats that differ from those of men. They correctly, and expertly, assemble an impressive suite of sex-differentiated phenomena directly or plausibly linked to female survival. We suggest that an adequate explanatory account must have life history tradeoffs between components tributary to reproductive success at its core, which include both survival and mating success. We discuss three examples of documented sex differences important for women's reproductive effort and survival: sexual disgust, fear of rape, and the cultivation of social bodyguards.

Sexual disgust

Women experience robustly higher levels of sexual disgust than men (Al-Shawaf, Lewis, & Buss, 2018; Crosby, Durkee, Meston, & Buss, 2020; Tybur, Lieberman, & Griskevicius, 2009). The target article attributes women's higher general disgust – which differs from more specific classes of disgust such as pathogen disgust, sexual disgust, or moral disgust – to their greater need to promote survival and avoid danger. One hypothesized function of sexual disgust, however, is mate avoidance. Importantly, this avoidance does not center around the avoidance of general danger or threats. Rather, sexual disgust motivates the avoidance of potentially harmful or sub-optimal mates (e.g., mates of lower mate value or mates unlikely to invest in a woman and her children), as well as mates who might be disease vectors (Crosby et al., 2020; Tybur et al., 2009). Sexual disgust may, therefore, protect women against death by avoiding these specific categories of mates. However, sexual disgust likely also protects women against reproductive costs including the accumulation of sexually transmitted infections or reputational damage, thus increasing her ability to secure high-quality mates in the future (e.g., Al-Shawaf et al., 2018). Together, this suggests that women's sexual disgust adaptations are at least somewhat domain-specific and contribute to components of both survival and mating success. It also highlights that a simultaneously broader and more domain-specific conceptualization – beyond the more general formulation of SAT – is needed for an adequate explanatory account of sex differences in disgust.

Fear of rape

Women face dramatically higher risks of sexual coercion and its accompanying hazards to survival and reproduction than men. Sexual conflict theory predicts that sex-specific adaptive problems create sex-specific selection pressures producing co-evolved defenses (Buss, 2017; Parker, 2009). Women's fear of rape is one hypothesized defense against sexual coercion costs.

Women's fear of rape protects against hazards associated with sexual exploitation including the circumvention of mate choice and physical damage incurred during rape (reproductive and survival costs, respectively; Perilloux, Duntley, and Buss, 2012). Women's fear of rape tracks the age at which victimization is most likely. For example, women between the ages of 19 and 35 express more rape fear than older women (Warr, 1985). Conversely, older women are more fearful of being mugged than being raped (Buss, 2021). Formidability mediates women's fear of rape such that women who perceive they could successfully escape an attack display less rape fear (Gordon & Riger, 1989; Pryor & Hughes, 2013).

While women's rape fear was not discussed in the target article, the authors reviewed several findings on women's greater levels of fear responding to social threats compared to men – a domain-general conceptualization. The specificity of findings of women's greater rape fear, such as predictable age gradients and female formidability findings, suggest that explanatory frameworks for women's fear require (1) their contribution to both survival and mating components of reproductive success, and (2) a more domain-specific conceptualization of fear beyond that offered by SAT.

Cultivation of social bodyguards

As a final example, consider the findings that women prioritize the cultivation of bodyguards in mate and friend selection. Women, more than men, prefer social alliances who are physically formidable (Meskelyte & Lyons, 2022; Snyder et al., 2011) – a sex difference not mentioned in the target article. Bodyguards, we suggest, have been and continue to be critical for women's survival and mating success. They offer unique functions including deterring physical and sexual assaults and reducing damage following assaults. These protections buffer against the survival and reproductive costs of sexual coercion (Buss, 2021) – again suggesting that explanatory accounts should consider the specific ways in which women's adaptations contribute to the multiple components of fitness, and tradeoffs therein, beyond the domain-general invocation of survival.

Conclusion

The target article describes an impressive array of documented sex differences in physiological, psychological, and emotional responses that are plausibly tributary to survival over human evolutionary history. We applaud the authors for expanding SAT to explain the evolution of these sex differences. We suggest that many important adaptive problems recurrently faced by women over evolutionary history contain fitness consequences for both survival success and mating success, and tradeoffs therein, and thus argue for a broader and more domain-specific conceptualization of these adaptations.

Financial support. No funding was received for this commentary.

Conflict of interest. We have no conflicts of interest to disclose.

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Women take risks to help others to stay alive

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doi:10.1017/S0140525X22000437, e135

Abstract

Evidence that women voluntarily expose themselves to some threats more than men do challenges the generalizability of the claim that women exceed men in self-protective responses. Examples include women's higher rates of living organ donation and rescuing Jews during the holocaust. In general, women's efforts to keep other people alive can take precedence over their efforts to protect themselves.

The principle that women, more than men, engage in self-protective reactions to threats is impressively documented by Benenson, Webb, and Wrangham, but their analysis is incomplete. They fail to acknowledge that women, sometimes more than men, put themselves in danger to preserve the lives of others or reduce their suffering. To contribute to a more complete account of the psychology of gender, I note and analyze some examples of women endangering themselves to protect others from suffering or death.

The first example derives from the excellent records for living organ donation, which consists primarily of kidney donation (Prasad, 2018; U.S. Organ Procurement and Transplantation Network, 2021). Medical considerations favor greater male donation, given men's higher rate of end-stage renal disease (Hsu, Iribarren, McCulloch, Darbinian, & Go, 2009) combined with the greater transplant success when donor and recipient sex are the same (e.g., Mudalige, Brown, & Marks, 2022). Nevertheless, since U.S. record keeping began in 1988, living kidney donations have been more common among women than men (60%), as are living donations of all organs (61%). This disparity has gradually increased in the United States, with 2020 data showing 65% women among living donors for kidneys and for organ donations overall. In addition, Kurnikowski et al. (2021) reported a 16-nation average of 55% female donors with considerable variation across these nations.

Donating an organ while alive presents nontrivial risks to donors. Even though death or major postoperative problems are rare (Choi et al., 2021), less serious complications, such as gastrointestinal discomfort, bleeding, respiratory difficulties, and surgical or anesthesia-related injuries are more common (e.g., 17% of donors in a U.S. study; Lentine, Lam, & Segev, 2019). Concerning long-term outcomes, living kidney donation is associated with glomerular hyperfiltration, predisposing donors for the development of chronic kidney disease, resulting in greater risk for end-stage renal disease (O'Keeffe et al., 2018). Specific to women, kidney donation is also associated with increased risk of preeclampsia, gestational hypertension, and preterm birth (Bellos & Pergialiotis, 2022). Finally, economic consequences can include lost wages, child care expenses, and out-of-pocket medical costs (Fu, Sekercioglu, Hishida, & Coyte, 2021). In summary, living organ donation can threatens donors' health and well-being beyond the immediate stresses of surgery.

Women placing themselves in danger to help others is also evident in the rescue of Jews in the occupied countries of Europe during World War II, actions often punishable by death or confinement in concentration camps (Becker & Eagly, 2004). The rescued Jews were often coworkers or friends of the rescuers, but some were strangers (e.g., Gilbert, 2003; Oliner & Oliner, 1988). Some rescuers gave short-term help, but many formed long-term relationships by hiding Jews within their own dwellings.

Records of such rescues exist in the Yad Vashem archive of data on non-Jews who rescued Jews. Becker and Eagly's (2004) analysis of these records suggested that women and men participated approximately equally overall. However, after excluding married couples from the rescuer samples because the relative responsibility of husbands and wives is unknown, significantly more women than men served as holocaust rescuers in the three occupied nations with the largest number of rescuers: Poland, the Netherlands, and France.

Volunteer activities typically attract more women than men and can present threats to volunteers, although these are rarely life-threatening. Notably, women are the majority of volunteers both in the United States (Turner, Klein, & Sorrentino, 2020) and worldwide (United Nations, 2018). The U.S. Peace Corps provides one example: Women constitute 65% of its volunteers (Peace Corps, 2021). This service is associated with health risks such as malaria and exposure to violence, which can include physical and sexual assault (Peace Corps, 2022). Infectious gastroenteritis was the most common illness among volunteers, followed by respiratory and pulmonary conditions, and behavioral health problems such as stress and anxiety (Peace Corps, 2018). Such humanitarian volunteering, which is disproportionately undertaken by women, thus can present threats to health and wellbeing (see also Dahlgren, DeRoo, Avril, Bise, & Loutan, 2009).

In summary, women are more likely than men to take risks in some settings in which their voluntary actions put them in some danger but directly benefit one or more other persons. Nevertheless, men are far more likely than women to risk their lives in extremely dangerous acts of rescue that are widely recognized as heroic (e.g., rescues in fires and serious accidents; Becker & Eagly, 2004). Causes may include not only men's greater physical prowess, but also their lower fearfulness in dangerous real-world settings and their greater tendency toward risky impulsivity (see review by Archer, 2019). Such actions can bring public recognition and even major accolades such as the Carnegie Medal for Heroism or the Canadian Medal of Bravery, which are received mainly by men (Eagly, 2009).

Other causes of sex/gender disparities in prosocial actions may reflect the greater tendency of women than men to exhibit empathy (see review by Archer, 2019), given that holocaust rescuing and humanitarian aid generally involve serving people who differ from oneself in characteristics such as religion and nationality. Such service may reflect universalistic themes of shared humanity that are common in religious and ethical systems (Post, 2002). If so, women's greater participation would be consistent with their greater religiosity (Beit-Hallahmi, 2003) and commitment to universalistic values (Schwartz & Rubel, 2005). Exploration of such influences and their possible links to evolutionary processes will contribute to understanding how women and men balance protecting themselves and taking risks that benefit others.

These demonstrated sex/gender differences in the types of risks undertaken disproportionately by women or men call for theories that encompass both nature and nurture. Accounting for sex and gender effects that vary across situations, cultures, and historical time benefits from regarding female and male behavior as regulated by nurture (e.g., gender roles and social expectations) and nature (hormonal and other biological processes) (Eagly & Wood, 2012, 2013). Such an integrative perspective could shed light on the question of why sex/gender differences in putting oneself in danger versus avoiding danger depend on the setting and the purpose of risky actions as well as well as the cultural context including its gender norms (Eagly, 2009).

Financial support. This research received no specific grant from any funding agency, commercial, or not-for-profit sectors.

Conflict of interest. None.

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An expanded “staying alive” theory (SAT) underplays complexity in *Homo sapiens*

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doi:10.1017/S0140525X22000449, e136

Abstract

The target article takes myriad human female patterns and aligns them as a unit emerging from an expanded version of “staying alive” theory (SAT). Females and males do differ, however, to treat the complexity of human response to threats as an explicit, evolved sexually dimorphic package is not reflective of current knowledge regarding health, sex/gender, and behavior in *Homo sapiens*.

Campbell's "staying alive" theory (SAT) argues human females produce stronger self-protective reactions to aggressive threats because self-protection has higher fitness value for females. The SAT's core assumption is that female and male humans are under such distinct evolutionary pressures that selection structures females' bodies and minds producing "unique" adaptations relative to males. The target article takes myriad patterns (behavioral, physiological, social, cultural) in human females and aligns them as a unit emerging from an expanded version of the SAT. Human females and males do respond in overlapping but different distributions to threats, pathogens, and related health challenges, but why this is the case is extremely complex and influenced by multiple and diverse social, historical, biological, and contextual variables.

There are patterned differences between males and females in many species. For example, most mammalian females live longer than males and there are a number of processes that affect female longevity including sex chromosome heterogamy/homogamy and telomere length (Xirocostas, Everingham, & Moles, 2020) and diversity and complexity in female life histories and behavior (e.g., Cooke, 2022; Morbeck, Galloway, & Zihlman, 1996). However, this article seeks not to complexify understandings of human behavioral variation, but to simplify them. And therein lies my first critique. Benenson et al.'s core assertion, and the assumptions of the SAT, rest heavily on the classic arguments by Bateman, Trivers, Hamilton, and others, about the relative costs of reproduction and their effects on parental investment and life histories. While these assumptions about evolutionary "costs" of being female and male remain common in biology textbooks, there are serious challenges to their precision and universality. Bateman's thesis, and work, is flawed and the realities of measuring and assessing relative costs of investment in reproduction and the implications/consequences for male and female behavior are complex (Drea, 2005; Gowaty, Kim, & Anderson, 2012; Tang-Martinez & Ryder, 2005). This complexity of patterns is especially true for humans (Borgerhoff-Mulder, 2004) given our complex neurobiologies (Eliot, Ahmed, Khan, & Patel, 2021), and distinctive sex/gender (Hyde, Bigler, Joel, Tate, & van Anders, 2018), life history (Sear, 2020), and morphological (Dunsworth, 2020) processes. Specifically, parental investment in humans is more complex than the authors of this article acknowledge, and the potential evolutionary implication of this reality is not taken into account in their assessments. While noting complexity in human reproductive processes the authors' still frame their argument around assumptions of costs/benefits arising from a nuclear family/two-adult-plus-offspring core reproductive unit, which is not the basal form of residence, social organization, or childcare in humans (Gettler, 2016; Rosenberg, 2021; Sear, 2021). They do acknowledge "grandmothering" and "cooperative care," but emphasize that females do most childcare in contemporary societies, and leave it at that. However, these assessments (from the HRAF and contemporary forager/horticulturalist groups) might not reflect the range and structures of human evolutionary, and contemporary, processes related to reproduction and energetic investments and their integration into the broader range of human social behavior (Borgerhoff-Mulder & Rauch, 2009; Fuentes, 2016; Fuentes & Wiessner, 2016; Spikins, 2015). There are other, equally valid, modes of explanation for human social organization and behavioral processes not solely grounded in assumptions of radically different evolutionary trajectories for females and males. The bottom line is that given current understandings of human evolution, physiology, and behavior one should question, and unpack, the basal framework of the SAT more extensively before building an entire thesis on it.

My secondary critique involves the evidence offered in support of the authors' argument. For example, the causes of mortality in Figure 2 are all prevalent with substantive impact primarily in the recent evolutionary moment (post-last demographic transition and post-industrial revolution). The WHO data suggest that on average females die later or less from certain diseases, but to understand morbidity and mortality of cancers or cardiovascular disease (CVD) or hepatitis A solely, or even primarily, as the outcome of evolved differences between male and female biology is to elide decades of research and scholarship on the myriad interconnecting social, economic, historical, and biological processes at play (Krieger, 2020). Similarly, coronavirus disease-2019 (COVID-19) is a particularly bad example as social structures and inequities are central in structuring outcomes of morbidity/mortality in pandemics/syndemics (Gravlee, 2020). Patterns of race, sex/gender, geography, region, and so on mortality from COVID are not the best locale to investigate female/male biological differences. Obviously, biological factors related to reproduction can be involved, but their relative contributions to the patterns and processes of the outcomes in the face of the societal/structural determinants of health are often relatively small, and often nonlinear. I do not have the space to engage the psychological and social behavior differences the authors review (e.g., smiling, politeness, sadness, anger, avoidance of confrontation, etc.). But, to see these as direct outcomes, and measures, of selection for behavioral differences in females and males due to differential patterns of reproductive investment is to ignore vast amounts of social scientific and ethnographic data/analyses on why/how humans smile, get mad, avoid specific kinds of social contexts, and so on. Of course, evolutionary histories affect these behaviors, but it stretches credulity to assume gender/sex differences in these behaviors are best represented as specific outcomes of targeted selection.

The authors are not ignorant of these critiques. In sections 7.2 and 7.3 they acknowledge complexity and state "we cannot specify which characteristics of sex/gender relate to self-protection." But if this is the case, isn't that all the more reason to avoid simple and strictly targeted selection models such as the SAT? It is likely that many of the processes highlighted, including aspects of SAT, are at play in contemporary humans. But to compartmentalize them as a unit and focus on only one selection model, as if its explanatory power is more meaningful, is to oversimplify and misrepresent the dynamics of the human processes being explored. In sum, to treat the complexity of human response to threats as an explicit, sexually dimorphic package being driven by a relatively simple selection hypothesis, the SAT, is not reflective of the immense body of knowledge regarding health, sex/gender, reproduction, and behavior in *Homo sapiens*.

Financial support. This research received no specific grant from any funding agency, commercial, or not-for-profit sectors.

Conflict of interest. None.

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Staying alive enhances both women's and men's fitness

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doi:10.1017/S0140525X22000553, e137

Abstract

We argue that Benenson et al. need to consider not only sex differences in the effects of care on offspring survival but also in age-specific fertility when predicting how longevity affects fitness. We review evidence that staying alive has important effects on both women's and men's fitness, and encourage consideration of alternative explanations for observed sex differences in threat responses.

In their target article, Benenson, Webb, and Wrangham (2021) expand upon Campbell's (1999) "staying alive" hypothesis, which reasons that because offspring survival is more tightly linked to maternal than paternal care, women should place a higher value on survival, and therefore exhibit stronger self-protective responses to threat. Core to this argument is the idea that, "survival is more fitness enhancing for females than males" (Benenson et al., 2021, p. 5). However, the original Campbell hypothesis, and in turn Benenson et al.'s use of it here, is not supported by our current understanding of human life histories. We therefore argue that the staying alive hypothesis is an insufficient explanation for their findings.

The staying alive hypothesis assumes that a reduction in lifespan is more damaging to women's fitness than to men's. Importantly, this requires not only (1) a differential effect of women's and men's mortality on the survival of *existing* offspring, but also (2) that this difference is not outweighed by a sex difference in the effect of longer lifespan on having *additional* offspring. Only when both of these assumptions hold is it possible that a gender-difference in the fitness value of longevity could drive differences between women and men in survival-promoting behaviors. Campbell's hypothesis focuses exclusively on the first assumption, ignoring the second. Here we use demographic data to examine the effects of survival on both the well-being of existing offspring and the prospects for future offspring.

First, we agree with Benenson et al. (2021) that mothers' care is more strongly correlated with offspring survival than is fathers'. Cross-culturally, maternal death has a much stronger negative effect on child survival than paternal death (Hill & Hurtado, 2009; Sear & Mace, 2008). The involvement of fathers in their children's upbringing varies across populations and paternal care can more easily be replaced by the care of another alloparent, such as a grandparent or other kin, than maternal care (Boyette, Lew-Levy, Sarma, Valchy, & Gettler, 2019; Meehan, Helfrecht, & Quinlan, 2014; Sear & Mace, 2008). Combined with the uncertainty men have of their genetic relatedness to alleged offspring, which can be a disincentive for investment, it follows that women's survival has greater effects on offspring well-being than men's, especially for young children. However, this fact alone is not enough to conclude that women's fitness is more strongly dependent on their survival than men's. For this, we need to assess the second assumption by considering sex differences in fertility across the life course.

In most human populations, men's fertility peaks later and declines more slowly with age than women's. Demographic data collected by Blurton Jones (2016) and further analyzed by Muller et al. (2020) indicate that among Hadza hunter–gatherers in Tanzania, men's age-specific fertility (ASF) is highest at 33, compared to 26 for women. Women's reproductive careers start early but halt with the onset of menopause around age 50, while men's begin later but are characterized by an extended fertile period lasting into their seventies (Muller et al., 2020). Demographic samples across a variety of subsistence modes show the same pattern, with men's ASF peaking later and declining more slowly than women's (Marlowe, 2000; Nisén, Martikainen, Silventoinen, & Myrskylä, 2014; Tuljapurkar, Puleston, & Gurven, 2007). This amounts to a substantial effect of later-life fertility on men's fitness. Furthermore, Tuljapurkar et al. (2007) show that these differences in men's and women's fertility curves impact senescence. Their model shows the human aging pattern reflects selection for survival for as long as men reproduce.

These differences in ASF curves reflect a variety of cultural and demographic processes: Men tend to be older than women at marriage, men are more likely to remarry than women, and in some societies polygyny allows older men to monopolize women of reproductive age. Furthermore, the same processes of sexual selection that Benenson et al. (2021) emphasize, where male competition for resources drives mating access, can lead to these age differences. It takes time to accrue wealth and status, shifting mens' reproductive careers later and enhancing prospects for later-life fertility when men are often in the best position to compete.

These data show that survival has different but important consequences for men's reproductive success. The potential for older-age fertility strongly increases the value of staying alive for men. How this weighs against women's payoffs for continued reproduction and childcare is an empirical question that cannot be answered easily with the currently available data. However, we posit that while for women longevity is critical for helping existing offspring to survive, for men staying alive longer can have important effects on the total number of offspring they father. Both factors need to be considered when determining whether survival is more fitness-enhancing for one sex than the other.

We encourage serious consideration of the alternative explanations offered by Benenson et al. (2021) when aiming to understand the drivers of the observed sex differences in self-protective behavior, including women's increased vulnerability to physical threats due to their smaller body size and lower status. Additional factors that we expect to play a role are cultural notions of masculinity and femininity that may shape how women and men respond to threatening situations as well as how they self-report behavioral and emotional responses to threats.

Financial support. The authors received no external funding specific to this research.

Conflict of interest. All authors declare that they have no conflicts of interest.

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Somatic maintenance/reproduction tradeoffs and human evolution

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doi:10.1017/S0140525X22000474, e138

Abstract

The authors propose that many morbidities higher in women than men are adaptations protecting survival, selected because survival has been especially crucial to mothers' reproductive success. Following their lead, I pursue variation in tradeoffs between reproduction and survival recognized by Darwin that were likely central to the evolution of many traits that distinguish us from our great ape cousins.

Benenson, Webb, and Wrangham's (BWW) extension of Campbell's (1999) staying alive theory (SAT) is a welcome elaboration of likely sex differences in fitness-related tradeoffs. Both the *Origin* (1859) and *Descent* (1871) show Darwin's own recognition of variation in tradeoffs that account for astonishing diversity in the living world. He lacked tools to understand how inheritance works but still saw enormous phenotypic consequences of sexual reproduction's "one mother, one father for each offspring" foundation. That foundation is now usually called the Fisher condition, as Fisher (1930) combined Mendelian inheritance with natural selection to show that each sex contributes half the ancestry of future generations. Although it is fertile females – not males – limiting the number of babies, offspring sex ratios are usually near even because two haploid gametes, ovum and sperm, form each diploid zygote. If males are rare, the *average* reproductive success of rare males is higher than the female average. Then mothers tending to produce more males average more grandchildren, erasing the male rarity.

The Fisher condition also explains why sex ratios in the fertile ages determine which strategies dominate mating competition. Campbell (1999) countered textbook claims that with typical sex roles males compete while females care: males are ardent, females coy. She cited Hrdy (1979, 1981, 1986), Smuts (1987, 1995), and Wrangham (1980) for evidence of libidinous and competitive female primates, with different resources limiting fitness for each sex: food and safety for females, paternities for males. Those differences contributed to Campbell's SAT and BWW's extension here.

Variations in tradeoffs between reproduction and survival were taken up by Williams' (1957) field-defining paper that explained why natural selection results in differing rates of aging across the living world. Williams (1966) later modeled costs to survival imposed by current reproduction showing selection favors a "normal reaction" adjusted to the actor's age and sex by fitness gains expected from additional allocation to current reproduction or to survival instead. Williams called the likely fitness value of the latter residual reproductive value (more on reproductive value in Hawkes, 2020a).

These tradeoffs are important for all sexual reproducers but their distinctive importance in human evolution is the topic here. Darwin saw phenotypic evidence of our phylogenetic closeness to great apes, now confirmed by genetics placing us all in the same hominid family. In all living hominids female fertility usually ends before age 50 – but great ape females age faster than women and usually die while still cycling. Humans differ in our postmenopausal longevity, later maturity, yet faster rate of baby production. A grandmother hypothesis to explain those distinctive traits uses ethnographic observations of grandmothers' foraging subsidies (Blurton Jones, 2016; Hawkes, O'Connell, & Blurton Jones, 1997, 2018) and theory developed to explain the broad variation in female mammal life histories (Charnov, 1991, 1993; Hawkes, O'Connell, Blurton Jones, Alvarez, & Charnov, 1998; O'Connell, Hawkes, & Blurton Jones, 1999). In two-sex agent-based models of that hypothesis, grandmothers' subsidies propel the evolution of a great ape-like life history to a human-like one (Kim, Coxworth, & Hawkes, 2012, 2014, 2019). Increased longevity also shifts the sex ratio in the fertile ages from the female-bias typical of mammals to the male-bias in humans as proportions of both post-fertile women and older still-fertile men expand (Coxworth, Kim, McQueen, & Hawkes, 2015). When mating sex ratios are female-biased, males pursuing multiple mates gain more paternities; with the bias reversed, claiming and guarding a mate against other males wins more paternities (Loo, Chan, Hawkes, & Kim, 2017a; Loo, Hawkes, & Kim, 2017b; Loo, Weight, Hawkes, & Kim, 2020; Loo, Rose, Hawkes, & Kim, 2021; Rose, Hawkes, & Kim, 2019; Schacht & Bell, 2016).

All of this follows ancestral grandmothers' subsidies adjusting the fitness maximizing tradeoffs between somatic maintenance and current reproduction. More somatic allocation results in more grandmothering subsidies, shortening birth intervals. Ancestral mothers' bearing next babies sooner poses survival challenges for their previous infants recognized by Hrdy (2009; see also Hawkes, 2014). She saw the precocious social responsiveness that makes human babies so engaging as an adaptive consequence of those challenges. Added to the maturity delaying effects of lower adult mortality, slower neural maturation expands final brain size and also proportion neocortex across the mammals (Finlay & Darlington, 1995; Workman, Charvet, Clancy, Darlington, & Finlay, 2013). The combination of earlier weaning with slower neural maturation would have wired distinctive priorities for shared understanding in ancestral infancy (Finlay, 2019; Finlay & Uchiyama, 2017; Hawkes, 2020b; Hawkes & Finlay, 2018).

BWW suggest their SAT's relevance to the male–female health-survival paradox: Where data are available, women's longevity is almost always greater than men's even though morbidities are higher in women than men (Alberts et al., 2014). If the morbidities BWW explore are actually protective that could resolve the paradox. If increased longevity was favored in our lineage as ancestral grandmothering displaced the independent mothering of other great apes, our postmenopausal life stage also had consequences for sexual selection (O'Connell, Hawkes, Lupo, & Blurton Jones, 2002). More fertile old men competed for paternities (Coxworth et al., 2015) with preferences for mating younger females that distinguish men from chimpanzees (Muller, Emery Thompson, & Wrangham, 2006, 2020). Ethnography shows older men usually hold substantial advantages over younger ones (Collier & Rosaldo, 1981; Hawkes, 2000; Marlowe & Berbesque, 2012; Rodseth, 2013). That alters males' fitness tradeoffs between current reproduction and somatic maintenance. Formal two-sex models of the grandmother hypothesis expose sexual conflict over longevity (Chan, Hawkes, & Kim, 2016, 2017; Kim et al., 2012, 2014) with male advantages for greater longevity pushing the compromise longevity higher than an equilibrium without males (Hawkes, 2020a).

If BWW's expansion of SAT brings more attention to the evolution of human postmenopausal longevity, more attention to consequences for paternity competition might follow. Yet the topic of sexual selection in human evolution can seem unwelcome where broader gender identities are now celebrated. Expanded appreciation of sexual fluidity can make Darwin's recognition of "competition among the males for possession of the females" seem to glorify toxic masculinity and obscure gender diversity. Yet Darwin's theory of natural selection including sexual selection is central to understanding human evolution. It helps explain pervasive conflicts of interest – and our distinct appetite for shared understanding, an appetite that inflates antagonisms – but can also defuse them.

Acknowledgments. I'm grateful to Megan Mullineaux and Jim O'Connell for insights and editorial advice.

Financial support. No special funding supported preparation of this comment.

Conflict of interest. I have no conflict of interest.

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"Staying alive" in the context of intimate partner abuse

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doi:10.1017/S0140525X22000504, e139

Abstract

Females are disproportionately affected by intimate partner abuse that can result in severe physical and mental harm. Benenson et al. provide little exploration of how female-evolved traits enhance females' survival in abusive relationships. Discussion centres on "why" females do not "just leave" an abusive relationship and the effectiveness of female-evolved traits in navigating intimate partner abuse over time.

Benenson et al. provide a compelling case that corroborates Campbell's "staying alive" theory. Substantial evidence was overviewed to support Benenson et al.'s claim that females invest more resources in reducing social conflict and protecting social bonds through various strategies (e.g., politeness, emotion identification) that enhance their survival. While I generally agree with Benenson et al.'s conclusions, I would like to extend them to the context of intimate partner abuse.

Benenson et al. acknowledge that females are disproportionately affected by gendered violence, particularly intimate partner abuse (Conroy, 2021). Yet it is unclear how female-evolved traits enhance their survival in abusive intimate relationships and if this is associated with "why" females do not "just leave" a relationship once it becomes abusive. Evidence suggests that the risk for violence is heightened when females leave or attempt to leave an abusive intimate relationship, with more than half of femicide being committed by a current or former intimate partner (Conroy, 2021; Petrosky et al., 2017). Femicide is found to be the leading cause of death of females in the pregnancy and post-partum period in the United States (Wallace, Gillispie-Bell, Cruz, Davis, & Vilda, 2021). Further, Johnson, Eriksson, Mazerolle, and Wortley (2019) found, in a sample of males incarcerated for femicide, that 50% did not perpetrate physical abuse in the year leading up to the femicide but exhibited coercively controlling behaviours (e.g., jealousy, stalking). Thus, severe violence and even femicide can occur even when escalating injuries from physical assaults are absent.

It could be argued that females do not immediately leave an abusive relationship as it could be safer to stay and wait for a less dangerous time for separation (e.g., once they have developed good coping skills, secured transportation/shelter/finances; Walker, 2009). During this time, they may use female-evolved traits to adapt to their environment. These include their enhanced sensitivity and reactivity for threat-related cues (e.g., abuser's expressions of anger) and proficiency for emotion identification that may aid them in learning their abuser's triggers to navigate the cycle of abuse and mitigate confrontation. While these strategies could diminish the severity of abuse episodes, they may not be self-protective over the long term. Particularly because females can be in an abusive relationship for extended periods (with studies reporting relationships lasting over 20 years; Eckstein, 2011; Humeny, Forth, & Logan, 2021), which heightens the risk for severe forms of abuse and detrimental consequences for females' mental and physical health (Mechanic, Weaver, & Resick, 2008). This includes acute and chronic pain from injuries (e.g., traumatic brain injury, maxillofacial injuries; de Macedo Bernardino et al., 2018; Smirl et al., 2019).

Even if abusers do not perpetuate physical abuse, chronic stress from the cycle of abuse and abusers' coercively controlling behaviours increase females' isolation (Walker, 2009) and susceptibility for mental health disorders, including post-traumatic stress disorder and depression (Karakurt, Patel, Whiting, & Koyutürk, 2017). Substantial evidence suggests post-traumatic stress disorder and depression impedes facial affect recognition (Cotter et al., 2018; Moser et al., 2015) and emotion regulation (Plana, Lavoie, Battaglia, & Achim, 2014; Vanderlind, Millgram, Baskin-Sommers, Clark, & Joormann, 2020), contributes to cognitive impairments (e.g., attention, working memory) and social withdrawal (Cotter et al., 2018; DePierro, D'andrea, & Pole, 2013; Schweizer & Dalgleish, 2011), and impairs the processing of "safe environments" (i.e., hinders processing of socially affirming information, reduces approach behaviours; Nawijn et al., 2015). Karakurt et al. (2017) found intimate partner abuse survivors demonstrated elevated rates of gynaecological and pregnancy-related problems, including injuries from sexual assault, sexually transmitted diseases, low birth rates, and late entry and/or inconsistent pre-natal care. Intimate partner abuse also contributes to reduced immune system functioning (Karakurt et al., 2017), decreased sleep quality (Lalley-Chareczko et al., 2017), and enhanced risk of cardiovascular disease and all-cause mortality (Chandan et al., 2020).

Since intimate partner abuse is associated with a heightened risk of all-cause mortality, staying in an abusive intimate relationship impedes survival and reproductive success. This is further evident via the effects of chronic stress and injury on mental and physical health, which appear to hinder the effectiveness of female-evolved traits (e.g., emotion identification proficiency) that may aid in navigating the cycle of abuse. Given the prevalence of intimate partner abuse and the effects it has on females' survival and reproductive success, Benenson et al.'s argument would benefit from including a discussion of how Campbell's "staying alive" theory applies to intimate partner abuse. One avenue would be to explore the association between female-evolved traits and their social networks that were established prior to the abusive relationship.

Benenson et al.'s findings parallel research that shows females have more intimate and reciprocal interpersonal relationships (Pearce, Machin, & Dunbar, 2021) and rely on a wider array of family and friends for mutual support than males (Conrad & White, 2010; Einolf, 2011). Females are also found to have more positive help-seeking attitudes than males (Mackenzie, Gekoski, & Knox, 2006). Males' adherence to traditionally masculine norms (e.g., risk taking, self-reliance, dominance) is associated with less help-seeking behaviours and declines in mental health (Wong, Ho, Wang, & Miller, 2017). Sylaska and Edwards (2014) found females had a higher rate of disclosing intimate partner abuse than males and tended to disclose to friends and female family members. Disclosure, coupled with the reception of social support (e.g., emotional or tangible forms, such as shelter, childcare, and/or financial resources), was predictive of improved mental health (Sylaska & Edwards, 2014). It has also been found to mitigate the isolation caused by intimate partner abuse and serve as a protective mechanism against continued abuse (Bybee & Sullivan, 2005). While females may have a wide social network and a willingness to disclose and seek help it is important that their support network is equipped with the appropriate resources to assist them in safely navigating and/or exiting an abusive relationship. Thus, continued education and community outreach, complete with community and institutional resources (e.g., risk assessments, reducing stigmatization, ensuring housing and employment stability), is necessary. These factors could provide survivors a safe environment for disclosure and help-seeking that may aid in mitigating the severe negative outcomes that can result from intimate partner abuse.

Financial support. This research received no specific grant from any funding agency, commercial, or not-for-profit sectors

Conflict of interest. None.

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Only as a last resort: Sociocultural differences between women and men explain women's heightened reaction to threat, not evolutionary principles

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doi:10.1017/S0140525X22000516, e140

Abstract

The target article proposed that women display greater self-protectiveness than men to major physical and social threats because such self-protective responses have higher fitness value for women than men. Rather than having evolutionary roots, we suggest the various physiological, behavioral, and emotional responses to social and physical threats exhibited more by women than men are instead rooted in sociocultural forces.

> "This biological principle [adaptation] should be used only as a last resort. It should not be used when less onerous principles … are sufficient for a complete explanation" (p. 11; George Williams, 1966, *Adaptation and Natural Selection*)

In their target article, Benenson, Webb, and Wrangham introduce an impressively broad model that emphasizes the evolutionary origins of gender differences in self-protective responses to major physical and social threats. Here we offer another way of understanding such differences. We propose the various physiological, behavioral, and emotional responses to social and physical threats exhibited more by women than men are instead rooted in status and power differences as well as gender stereotypes, roles, and norms.

Social role theory provides the theoretical scaffolding for our argument and suggests that gender differences arise through gender socialization and the placement of men and women in different roles in society (Wood & Eagly, 2002). According to the theory, basic biological differences between women and men, including differences in childbearing, physical strength, and size, led to a historical and contemporary division of labor (i.e., different social roles) in society. Social structural features, particularly power and status differences associated with the different social roles women and men occupy, are the primary cause of observed differences between the sexes. This division of labor accounts for why women are more communal and men are more agentic. Women are primarily responsible for domestic labor and childcare, even when employed, leading them to be more communal. Men are primarily responsible for work, leading them to be more agentic. This division of labor leads to different beliefs about women and men (e.g., stereotypes) and how they should behave (e.g., gender roles and norms). From this view, women's self-protective responses to social and physical threat result from sociocultural forces, including women's lower status and power in society, gender stereotypes, and gender roles and rules.

In what follows we briefly review evidence consistent with this view. Before continuing, however, it is important to point out what we are not saying. We are not disputing that the human brain is a product of evolution. That is trivially true. Social role theory is a "biosocial constructionist theory" that proposes that cultural processes interact with evolutionary forces (Eagly & Wood, 2013; Wood & Eagly, 2002). The question is how and in what ways evolutionary forces shaped women and men, not about whether such forces had an influence.

The authors of the target article cite research showing that women report greater pain, both when experimentally induced in the laboratory and clinically. The authors suggest that this is an evolved self-protective response to physical threat on the part of women, however, research demonstrates such differences are mediated, in part, by gender roles (Sanford, Kersh, Thorn, Rich, & Ward, 2002). In this case, gender differences in femininity predicted pain tolerance and perception. A similar role for gender roles in pain can be found across many studies (Fillingim, King, Ribeiro-Dasilva, Rahim-Williams, & Riley, 2009). Further, both women and men have the stereotype that women are more sensitive to pain and more willing to report pain. Such stereotypes predict sex differences in pain tolerance and perception (Fillingim et al., 2009).

The authors cite research showing that women tend to smile more, they are more polite, and they are better able to identify other's emotions during social interaction than men. The authors suggest these differences are an evolved self-protective response to social threats on the part of women. However, research shows that such differences are shaped by sociocultural forces. There are strong sex-based norms for smiling, with smiling being more acceptable for women because women are supposed to be communal and expressive (LaFrance, Hecht, & Paluck, 2003). Women also smile more than men due to their social roles within society. Sex differences in smiling are reduced when men and women occupy the same social role (LaFrance et al., 2003). Research demonstrates that gender roles and rules can explain women's greater ability to decode the emotional expressions of others (Brody & Hall, 2008), and their greater use of tentative speech (Kalbfleisch & Herold, 2006).

The authors argue that greater self-reports of negative emotion by women reflect a greater reaction to threat, however great caution should be taken when interpreting sex differences in self-reported emotion. Many studies show that on retrospective self-reports women report greater general emotionality as well as experiencing specific emotions with greater frequency. These differences disappear when emotional experiences are measured in the moment (i.e., online emotion reports; Robinson & Clore, 2002). Daily diary studies that capture emotion dynamics in real time, for example, find no differences in the emotional lives of women and men (Barrett, Robin, Pietromonaco, & Eyssell, 1998). In other research, women and men in the laboratory played a word game competition where some participants were asked their emotional reactions immediately after the game, and others reported them a week later. Results showed no gender differences in immediate online emotional reports, but a stereotypic pattern of emotional report was evident at 2 weeks (Robinson, Johnson, & Shields, 1998). These and other studies suggest that the emotional lives of women and men are nearly identical.

Many of the various other self-protective reactions mentioned in the target article have also been explained via mechanisms other than evolutionary ones. Women's lack of social power and gender roles makes them more vulnerable to depression (Nolen-Hoeksema, 2001). Due to their lower status and gender roles, they face more chronic strains and stressors in their lives than men, making them more likely to develop depression since the experience of stressful life events strongly contributes to depression. Gender roles and rules also play a role in gender differences in anxiety disorders (McLean & Anderson, 2009). Increased stress can also have detrimental impacts on immunity, contributing to differences between women's and men's stress responses (Verma, Balhara, & Gupta, 2011).

We conclude by suggesting the authors may have prematurely jumped to evolutionary conclusions when other sufficiently complete explanations, in this case gender differences in status and power, gender roles and rules, are readily available.

Financial support. This research received no specific grant from any funding agency, commercial, or not-for-profit sectors.

Conflict of interest. None.

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Harm or protection? Two-sided consequences of females' susceptible responses to multiple threats

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doi:10.1017/S0140525X22000607, e141

Abstract

The target article presented a plausible argument that females' susceptibility to threats might be self-protection for *staying alive*, but some evidence requires scrutiny. We need to consider (1) the biases of narrative reviews, (2) subjective life quality, and (3) the shadow side of extreme reactions to threats before concluding that females' threat-based response is a self-protection mechanism that promotes survival.

We want to congratulate Benenson, Webb, and Wrangham (2021) with their important Campbell's (1999) "staying alive" theory and why this may explain the gender/sex gap in psychopathology. However, we also have some concerns about this approach. Although the narrative approach these authors used is often used to summarize a research field, the criteria for selection of studies to include are not explicit (Cuijpers, 2016). More detailed criteria for which studies were included and which not would be a helpful addition for readers to get an overall impression of this research field.

It is well-known that the sex/gender binary has been extensively questioned and studied (Morgenroth & Ryan, 2021) by neuroscientists, psychologists, and researchers in behavior and neuroendocrinology (Li, Yuan, & Lin, 2008; Yuan, Luo, Yan, Meng, Yu, 2009; Hyde, Bigler, Joel, Tate, & van Anders, 2019; Lin et al., 2021). Hence, to minimize bias from the sex/gender binary, it is also important to consider multiple genders' responses to threats and their associations with life-related properties instead of focusing on sex/gender comparisons between females versus males only. Moreover, we propose reconsidering the structure of "staying alive" beyond survival or life expectancy to get a more comprehensive relevant premise and evidence base of a field for further research. Some relevant evidence on these issues exists that we briefly review below.

As the target article reviewed, accumulated evidence has shown that women live longer than men as measured by life expectancy, but they were more likely to experience negative emotions and illness. For life expectancy, it is predicted that the female advantage will shrink by 2030 in at least 30 countries (Kontis et al., 2017). Furthermore, there is another authoritative health index, the so-called "healthy life expectancy" (Salomon, Mathers, Murray, & Ferguson, 2001), focusing on the quality of life spent in a healthy state (Robine, Michel, & Branch, 1992). This index indicates a gender gap at just a 0.9-year difference in favor of women, which is considerably smaller in terms of healthy life years than overall life expectancy (OECD, 2013). Therefore, one reservation is that longer life expectancy is a quantified form of, but may not be synonymous with, staying alive. It is also essential to consider the associations of qualitative facets of staying alive (e.g., life satisfaction, quality of life, subjective well-being, etc.) with susceptible responses to threats.

The target article also reviewed convincing evidence on female protective responses (e.g., smiling, politeness, identification of others' emotions) to social threats, contributing to psychological well-being and quality of life. Smiling, politeness, and compassion are indeed positive signs of prosocial intentions and increase socially perceived attractiveness (Gangestad & Scheyd, 2005), which helps gain more social support in most aspects of life (Becker & Srinivasan, 2014; DeYoung, Quilty, & Peterson, 2007). Support from friends has been found to be positively linked with maternal life satisfaction (Luthar & Ciciolla, 2015). Perceived social support benefits single mothers' well-being, and is linked with positive development outcomes in the child (Taylor & Conger, 2017). In contrast, lower maternal life satisfaction leads to a high risk of child behavior problems in the future (Totsika et al., 2013). These pieces of evidence also support female responses to threats as a self-protective consequence for themselves and their children.

However, the evidence does not comprehensively support the protective role of female reactions to some socioeconomic threats. For example, in the medical workplace, burnout affects nearly half of US physicians and disproportionately affects women who report lower satisfaction with the pressure of work–life integration than men (Cunningham, 2008). Women are more likely to experience unemployment than men, inhibiting subjective well-being and leading to physical and mental diseases (Iacovides, Avidon, Bentley, & Baker, 2014).

Several clinical conditions (e.g., depression and anxiety) occur more frequently in women than men. How does the staying alive theory explain the reproductive significance of mood and anxiety disorders caused by extreme responses to threats? Perinatal depression, a depressive episode during pregnancy and after the birth of a child is a good example (Drury, Scaramella, & Zeanah, 2016). It is estimated that around one in seven women in high-income countries and one in 10 women in low-income countries are affected by perinatal depression (Woody, Ferrari, Siskind, Whiteford, & Harris, 2017). Perinatal depression has clear negative effects on the infant and child development in cognitive, emotional, behavioral, and physical outcomes and leads to a considerable reduction in maternal quality of life (Cuijpers et al., 2021). Complications of untreated perinatal depression include maternal suicide (Slomian, Honvo, Emonts, Reginster, & Bruyère, 2019). Therefore, it appears to threaten instead of protecting new female parents and their offspring's survival and fitness.

In summary, it is easy to find counterexamples to dispute the viewpoint that females' reactions to threats are adaptive self-protection. Meanwhile, the limitations of the staying alive theory for interpreting the clinical consequences of extreme reactions to threats should be identified with caution. It seems that susceptible responses to threats have both protective and harmful impacts on female life expectancy and life quality. We would like to acknowledge the authors have outlined the abundant essential evidence that serves important roles for future studies to explore, identify, and manipulate the potential moderators for promoting self-protective aspects and reducing negative impacts.

Financial support. The commentary is supported by the following: Ministry of Education Key Projects of Philosophy and Social Sciences Research [grant number 21JZD063]; Guangdong Key Project in "Development of new tools for diagnosis and treatment of Autism" [2018B030335001]; National Natural Science Foundation of China [NSFC31871130]; the National Science and Technology Innovation 2030 – Major program of "Brain Science and Brain-Like Research" [2021ZD0200520 and 2021ZD0200531]; Shenzhen Science and Technology Research Funding Program [JCYJ20200109144801736].

Conflict of interest. None.

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Female advantage in threat avoidance manifests in threat reaction but not threat detection

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doi:10.1017/S0140525X22000462, e142

Abstract

Threat avoidance involves both detection of a threatening stimulus and reaction to it. We demonstrate with empirically validated stimuli (that are threatening, nonthreatening-negative, neutral, or positive) that threat detection is more pronounced among males, whereas threat reactivity is more pronounced among females. Why women are less efficient detectors of threat challenges Benenson et al.'s conceptual analysis.

Benenson et al. suggest that females have a stronger self-protective capacity to avoid survival threats than do males. A more general threat-superiority literature suggests that humans inherited a neural architecture that preferentially processes and responds to immediate survival threats (of phylogenetic or ontogenetic origin; Blanchette, 2006; March, Gaertner, & Olson, 2018a, 2018b; LeDoux, 2012; Öhman & Mineka, 2001). Such threat-superiority manifests as earlier detection and stronger responses to threatening than non-threatening stimuli. For example, March, Gaertner, and Olson (2017) empirically validated four categories of stimulus images – threatening (e.g., snarling predators, gunmen), nonthreatening-negative (herein "negative," e.g., bugs, wounded animals), positive (e.g., puppies, babies), and neutral (e.g., doorknobs, mugs) – and found that the threatening stimuli were identified faster, more frequent targets of initial eye-gaze, and elicited stronger startle-eyeblinks. Conceptually similar patterns occur when threat superiority is isolated from the opposing effect of conscious attention by presenting stimuli outside conscious perception (i.e., by using masked presentations at 14–21 ms; March, Gaertner, & Olson, 2022). Not considered by the threat-superiority literature, however, is the possibility of a sex difference favoring females.

Benenson et al. focused primarily on reaction to, rather than the detection of, threat. Accordingly, we reanalyzed data from four of our studies: two that assessed stimulus detection and two that assessed stimulus reaction. As a caveat, we powered our studies to test within-subject effects of the stimuli not between-subject effects such as sex. Moreover, sex imbalances among our college-student samples compromise inferential tests of sex differences. Consequently, we focus on the effect size of the sex difference (Table 1).

The stimulus detection studies in the top half of Table 1 used visual search and eye-tracking tasks. Each trial of visual-search presented a 3 × 3 matrix containing a central "X" surrounded by eight stimuli. On congruent trials, stimuli were all threatening, all negative, all neutral, or all positive. On the critical incongruent trials, either one threatening or negative stimulus was embedded among seven positive or seven neutral stimuli. Participants pressed one of two keys to indicate whether the stimuli were all the same or not. Males were faster than females to detect the incongruent threatening stimulus and the incongruent negative stimulus. Each trial of the eye-tracking task presented a pair of stimuli from different categories (e.g., threat and negative) and assessed at which stimulus the participant first gazed. Males were more likely than females to first gaze at a threatening than negative or neutral stimulus, and to first gaze at a negative than positive stimulus, with negligible differences on the remaining

Table 1 (March and Gaertner). Sex differences in stimulus detection and reaction

Source	Task	F_n	M_n	Stimulus	*d*
Stimulus detection					
Study 1[a]	Visual search	35	55	Thr	−0.59
				Neg	−0.54
Study 2[a]	Eye tracking	29	34	Thr vs. Neg	−0.18
				Thr vs. Neu	−0.16
				Thr vs. Pos	−0.03
				Neg vs. Pos	−0.15
				Neg vs. Neu	−0.09
				Pos vs. Neu	0.08
Stimulus reaction					
Study 3[a]	Startle eyeblink	94	28	Thr	0.35
				Neg	−0.20
				Neu	−0.18
				Pos	0.08
Study 2[b]	Startle eyeblink	70	30	Thr	0.40
				Neg	0.27
				Neu	−0.17
				Pos	−0.38

Note. F_n = female sample size; M_n = male sample size; Thr = threat; Neg = negative; Neu = neutral; Pos = positive. Effect size *d* is scored so positive values reflect a stronger female than male response and is the difference of the female mean minus the male mean divided by their pooled standard deviation with the exception of the eye-tracking data for which we converted the odds ratio of the sex difference in the tendency to first gaze at the stimulus listed first vs. second to *d* as ln(OR)/1.65 (Sánchez-Meca, Chacón-Moscoso, & Marín-Martínez, 2003). Sample size discrepancies from the source are because of currently excluding participants who did not specify their sex and the reversed labeling of sex frequencies in study 1 of March et al. (2017).

[a] March et al. (2017).

[b] March et al. (2022).

pairings. These data suggest that males have an advantage over females in the detection of threatening stimuli.

The stimulus reaction studies in the bottom half of Table 1 assessed startle eyeblink – a reflexive response measured by electromyography of the orbicularis oculi muscle (Blumenthal et al., 2005). Each trial presented an image from one of the four stimulus categories for 6,000 ms (in the first study) or 21 ms (in the second). On critical trials, a 100 dB noise blast was presented via headphones 2,000–4,000 ms after stimulus image onset to trigger a startle-eyeblink. Females responded with a larger startle-eyeblink than did males when the noise blast was paired with threatening stimuli in the first and second studies and with negative stimuli in the second study. Alternatively, males responded with a larger startle-eyeblink than did females when the noise blast was paired with neutral stimuli in the first and second studies, with negative stimuli in the first study, and with positive stimuli in the second study. The only consistent pattern across studies favoring females was in response to threat, which supports Benenson et al.'s argument. That a consistently stronger female response did not occur to other stimuli rules out the alternative of an invariantly stronger female response. The stronger female response appears cued to immediate survival threats.

Our data support Benenson et al.'s argument in regard to reaction to threat but not in regard to threat detection. The only evidence Benenson et al. considered that could be construed as threat detection was their section on pain tolerance. A sex difference in self-reported pain, however, could be compromised by gender role expectations that differentially influence male versus female reports (Robinson, Gagnon, Riley, & Price, 2003). Of course, Benenson et al. did not buttress their argument solely with self-report. Nonetheless, gender expectations could compromise much of the self-report data they used (e.g., such as emotions, sleep disruption, and picture aversion; Grossman & Wood, 1993; Wong, Pituch, & Rochlen, 2006). Fortunately, the threat detection and reaction tasks that we employed are not easily compromised by gender role expectations. Reanalysis of our data reveals a stronger female self-protective capacity to avoid survival threats in regard to stimulus reaction but not stimulus detection. Why males are more efficient than females at detecting immediate survival threats requires further consideration by Benenson et al.

Financial support. This research received no specific grant from any funding agency, commercial, or not-for-profit sectors.

Conflict of interest. None.

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Women need to stay alive and protect reproductive choice

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doi:10.1017/S0140525X22000486, e143

Abstract

Defense of reproductive choice is an important motivation in women's self-protection psychology for which the "staying alive theory" cannot fully account. Evidence indicates that some elements of women's self-protection psychology function to protect reproductive choice rather than survival, or may be equally well explained by either motivation. Integrating perspectives will result in greater explanatory breadth and precision in theory testing.

Benenson et al. propose an extension of Campbell's (1999) staying alive theory (i.e., SAT), and marshal an impressive array of empirical data to support their claims. We agree with the authors' theoretical premise, but suggest that in order to fully capture females' self-protection psychology, the SAT must also address the importance of *protecting reproductive choice*. A key means by which females increase reproductive fitness is through strong mate preferences (Trivers, 1972). Yet, female choice is often thwarted by males through sexual coercion and aggression (e.g., Brown, 1952; Chagnon, 1988; Minturn, Grosse, & Haider, 1969; Palmer, 1989; Rozée, 1993; Sanday, 1981). Converging lines of evidence suggest that this intersexual competition has generated selection pressure for a psychological system in women designed to protect reproductive choice (reviewed in McDonald, James, & Roberto, 2021). This is an important extension of the ideas proposed by Benenson et al. for each of the reasons outlined below.

Not all self-protection functions to promote survival

Women express greater fear of personal crimes (e.g., murder, assault, rape, burglary) than men (e.g., Ferraro, 1996; Franklin & Franklin, 2009), despite the fact that women are victimized less frequently for most such crimes, outside of rape (Craven, 1997; Rennison & Rand, 2003). Although these data align with the SAT, women's greater fear of personal crimes appears to be driven more by the desire to protect reproductive choice than to stay alive. Indeed, sex differences in fear of personal crimes are eliminated or reversed when *fear of rape* is statistically controlled, but not fear of murder (Ferraro, 1996; but see Lane & Meeker, 2003). Described as the "shadow of sexual assault," women's greater fear of personal crimes is largely driven by a fear that those crimes will co-occur with rape (Ferraro, 1995, 1996; Fisher & Sloan, 2003; May, 2001; Warr, 1984, 1985). Moreover, women's fear of rape often matches or exceeds their fear of murder (Ferraro, 1995, 1996; Warr, 1984). In short, the SAT is not sufficient to fully explain the sex difference observed in fear of personal crimes.

Women's fear of rape and their history of sexual assault are also associated with self-protection behaviors aimed at reducing the likelihood of becoming the victim of violent crime. For example, women consume true crime media with greater frequency than men, particularly when it has high information value for self-protection (e.g., when it features female victims, describes the perpetrator's motives, and provides tips for escape; Vicary & Fraley, 2010). This desire for self-protective information appears to be rooted in women's fear of rape. Indeed, women who express a stronger fear of rape consume true crime media with greater frequency, and do so with the explicit motivation to learn strategies for defensive vigilance (McDonald et al., 2021). Although consumption of true crime media may cause elevated rape fear, it is plausible that the causal pathway is bidirectional. To that point, women's sexual assault history (unlikely to be the causal outcome of true crime consumption) is positively associated with women's frequency of true crime media consumption and the motivation to consume it for the purpose of defensive vigilance. In total, there is good evidence to suggest that women who are particularly fearful of rape engage in behaviors to protect their reproductive choice.

A number of studies have also documented that women's self-protection behavior varies as a function of conception risk across the menstrual cycle, a key factor that exacerbates the reproductive cost of sexual assault. For example, studies have shown that women at high risk of conception, relative to women at low risk, are less likely to engage in sexually risky activities (Bröder & Hohmann, 2003; Chavanne & Gallup, 1998), infer greater threat from male strangers (Fessler, Holbrook, & Fleischman, 2014; Garver-Apgar, Gangestad, & Simpson, 2007), exert greater handgrip strength in response to sexually threatening contexts (Petralia & Gallup, 2002), and express greater bias against outgroup males (McDonald, Asher, Kerr, & Navarrete, 2011, 2015; Navarrete, Fessler, Fleischman, & Geyer, 2009). While a general motivation for self-protection should be constant across the menstrual cycle, the motivation to protect reproductive choice is most pertinent on days when conception risk is elevated, indicating that these findings are better explained by the motivation to protect reproductive choice than the SAT.

The functions of self-protection behaviors may not be mutually exclusive

Some of the data presented by Benenson et al. cannot be easily explained by a motivation to protect reproductive choice (e.g., women's heightened immune response and lower pain threshold), but others are somewhat ambiguous. For example, the higher rate of nighttime awakenings among girls versus boys, and the onset of this sex difference during puberty, suggests that such awakenings could also be explained by the protection of reproductive choice. Given social and legal sanctions against rape, it is a behavior often hidden at night (Waterhouse, Reynolds, & Egan, 2016). Indeed, "nightcrawling" is a common form of rape in small-scale societies in which men trespass into women's homes to sexually coerce, rape, and abduct women (Rozée, 1993; Sanday, 1981).

Many of the findings highlighting women's tendency to engage in behaviors that reduce the risk of interpersonal conflict, such as smiling, politeness, recognizing negative emotions, avoiding confrontation, and experiencing more threat-responsive negative emotions, may also be seen as attempts to reduce the risk of sexual aggression – particularly given the overlap in women's fear of crime and rape. Similarly, the tendency for women to score more highly on measures of neuroticism may simultaneously function to protect reproductive choice, given research showing positive associations between neuroticism and women's fear of rape (McDonald, Coleman, & Brindley, 2019).

Conclusion

The expansion of the SAT is both a useful and powerful means of explaining women's self-protective psychology. However, a pure emphasis on survival without the integration of the importance of protecting reproductive choice, leaves some aspects of women's self-protection unexplained. Moreover, integrating reproductive choice as an additional motivation for self-protection would encourage research to engage in more precise theory testing to determine whether the pattern of data is better aligned with general self-protection motives or domain-specific self-protection attuned to threats against reproductive choice.

Financial support. This research received no specific grant from any funding agency, commercial, or not-for-profit sectors.

Conflict of interest. None.

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Biological sex, by-products, and other continuous variables

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doi:10.1017/S0140525X22000425, e144

Abstract

Sex/gender is a continuous variable that researchers frequently treat as dichotomous. This practice can mask continuous underlying adaptive traits and yield spurious dichotomous "sex differences." As such, many sex differences in self-protection may be evolutionary by-products of underlying adaptations rather than adaptations themselves. Binary analysis of continuous sex/gender is ill-considered science that can contribute to inequality and counterproductive public policy.

It's a convenient shorthand to treat sex/gender as dichotomous, and Benenson et al. necessarily rely on studies that use this shorthand exclusively. However, it's important to emphasize that sex/gender is, in fact, a multifaceted bimodal continuous variable. The authors have done outstanding work synthesizing copious cross-cultural data, unequivocally demonstrating stronger self-protective reactions in females. However, whether these differences are truly a "series of evolved female adaptations" that constitute an adaptive survival strategy, or a collection of adaptations and evolutionary by-products remains in question.

Are all sex differences adaptations? Sex differences in a psychological trait can serve as supporting evidence for an evolved psychological mechanism. However, sex differences are neither necessary nor sufficient to identify a psychological adaptation or differentiate a purported adaptation from an evolutionary by-product (an evolved trait inexorably linked with an adaptation). It's likely that some of Benenson et al.'s proposed female self-protection adaptations have continuous factors other than sex underlying the "sex differences" and that some of these differences are (either functionless or fitness-enhancing) evolutionary by-products of these underlying factors.

For example, Benenson et al. note that women "overestimate the speed of incoming stimuli" more than men (sect. 7.1).

Auditory perception research shows that both sexes perceive incoming sound sources as faster and closer than equivalent receding sounds and as arriving sooner than they actually do (Neuhoff, 2001, 2016; Neuhoff, Planisek, & Seifritz, 2009). This "auditory looming bias" is an adaptation that provides a margin of safety and affords more time than expected to prepare for a threat's arrival (Neuhoff, 1998). Women exhibit a larger bias than men and are therefore afforded greater self-protection (Neuhoff, Hamilton, Gittleson, & Mejia, 2014; Neuhoff et al., 2009; Schiff & Oldak, 1990). If we stop there, we have a story that fits nicely with "self-protection as an adaptive female strategy."

However, subsequent work showed that physical strength is correlated with the looming bias. The more formidable one is, the smaller the bias (Neuhoff, Long, & Worthington, 2012). Importantly, this relationship persists even when within-sex correlations are calculated. Thus, strength is more important than biological sex in explaining reactions to looming sounds. The sex difference is simply a by-product of a mean sex difference in strength, indicating vulnerability to threat. Sample sizes in these looming studies are not as large as those in the work reviewed by Benenson et al., and this sex difference was not included in their analysis. Nonetheless, other sex differences in self-protection may also be by-products of a more explanatory continuous variable.

For example, Benenson et al. identify sex differences in pain as a female self-protective adaptation. However, men and women also differ in sex hormone levels. Although the effects of estrogen and testosterone on pain perception are complex, there is ample evidence showing that under many conditions, testosterone decreases responses to pain, while estrogen increases it (Craft, 2007; Flake, Hermanstyne, & Gold, 2006; Ji, Hu, Li, & Traub, 2018; Ji, Tang, & Traub, 2008; Lesnak, Inoue, Lima, Rasmussen, & Sluka, 2020; Schertzinger, Wesson-Sides, Parkitny, & Younger, 2018). In animal models, ablation of estrogen receptors eliminates sex differences in pain entirely (Li et al., 2009). In humans, testosterone therapy successfully relieves fibromyalgia pain (Dubick, Ravin, Michel, & Morrisette, 2015; White et al., 2015).

Thus, reproductive hormones (whose main evolutionary job is facilitating *reproduction*) can plausibly explain sex differences in pain perception. This hypothesis is buttressed by data showing little evidence of sex differences in pain among children (Boerner, Birnie, Caes, Schinkel, & Chambers, 2014). Importantly, these pain–hormone relationships are robust *within*-sex (Ivkovic, Racic, Lecic, Bozovic, & Kulic, 2018; Kato et al., 2020). The dichotomous shorthand that we use for "sex" obscures the bimodal yet continuous underlying potential cause of the "sex difference."

Rather than an adaptation, sex differences in pain may be an exaptation of the effects of reproductive hormones. Variability in sex hormones may indeed currently enhance female fitness in response to pain. However, the main adaptive problem sex hormones solved was facilitating sexual reproduction. This reasoning applies to many of Benenson et al.'s other proposed female self-protection adaptations that are influenced by hormones, including immune function, fear, stress, autoimmune disorders, responses to vaccines, depression, anxiety, and emotion recognition (Amiaz & Seidman, 2008; Dirlikov, Lavoie, & Shem, 2019; Glover et al., 2013; Hermans, Putman, Baas, Koppeschaar, & van Honk, 2006; Maeng & Milad, 2015; Rehbein et al., 2021; Rosen, Ham, & Mogil, 2017; Ruggieri, Anticoli, D'Ambrosio, Giordani, & Viora, 2016). Underlying continuous factors might also explain responses to some social threats. For example, sex differences in smiling may be explained by variability in dominance and affiliation, as even within-sex variability in smiling predicts physical dominance (Hess, Adams, & Kleck, 2005; Ketelaar et al., 2012; Kraus & Chen, 2013).

Abraham Maslow famously said, "If all you have is a hammer, everything looks like a nail." This quote perfectly encapsulates the current state of research on sex differences. Benenson et al. acknowledge the dubious wisdom of treating sex/gender as binary, but it was the only type of data available for their synthesis. Historically, researchers (myself included) have failed to treat sex/gender as continuous. Thus, the only analysis tool currently available is a "binary hammer" that destroys the nuance of the continuum and masks other potentially more explanatory constructs.

As scientists, we need to do better to examine sex/gender as a multifaceted continuous variable because it's good science and it has critical implications for equality and public policy. Dichotomizing continuous variables obscures individual differences and nonlinear relationships, underestimates effect size, reduces statistical power, and decreases reliability (MacCallum, Zhang, Preacher, & Rucker, 2002). This mismeasurement leads to poor policy recommendations and greater inequality. For example, in a startling commentary on Campbell's (1999) original "staying alive" target article, which posited greater female self-protective behaviors in risk-taking and aggression, Browne (1999) concluded that perhaps women were not fit to serve in military combat or as business executives. Clearly, looking at continuous data through a dichotomous lens misses a richer explanation of the phenomena (Cameron & Stinson, 2019).

Acknowledgments. I am grateful to Bryan Karazsia and Laura Sirot for their cogent comments.

Financial support. This research received no specific grant from any funding agency, commercial, or not-for-profit sectors.

Conflict of interest. None.

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The pregnancy compensation hypothesis, not the staying alive theory, accounts for disparate autoimmune functioning of women around the world

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doi:10.1017/S0140525X22000589, e145

Abstract

The pregnancy compensation hypothesis provides a mechanistic explanation for the evolution of sex differences in immune system functioning, the excess of women experiencing autoimmune disease, and why this is observed only in industrialized nations; none of which can be explained by the staying alive theory, as proposed by the authors of the target article.

In the target article, self-protection as an adaptive female strategy (Benenson et al., this issue), the authors extend the staying alive theory (SAT; Campbell, 1999) to be a global theory explaining sex differences in physiology and genetics, and gender differences in culture, without describing mechanisms for how each of these could have evolved under the SAT, nor whether these observations are also consistent with other theories. In particular, we take issue with the supposition that sex differences in immune function are explained by the SAT. In contrast, the pregnancy compensation hypothesis (Natri, Garcia, Buetow, Trumble, & Wilson, 2019) provides mechanistic explanations for the evolution of sex differences in immune function and differences in industrialized and non-industrialized nations. We explain our critiques below.

First, sex differences in immune function are rampant in industrialized populations, with approximately 80% of autoimmune diseases occurring in women. In general, women are nine times more likely than men to develop autoimmune diseases (Ngo, 2014). For example, women have a higher rate than men for rheumatoid arthritis with a 7:1 female to male ratio (National Institute of Arthritis and Musculoskeletal and Skin Disease, 2019) and Alzheimer's disease with a 2.3:1 female to male ratio (Mouton et al., 2018). While there are autoimmune diseases in which men have a higher incidence rate than women (e.g., ankylosing spondylitis; Jørgensen, Pedersen, Nielsen, Jacobsen, & Frisch, 2012), these are less common in the population. Thus, there are many more autoimmune diseases with a higher incidence in women and there are many more women affected by these diseases than men.

Importantly, the sex difference in autoimmune disease has not been observed in non-industrialized populations, which are more likely to represent an ancestral disease condition. In fact, autoimmune diseases, in general, are less prevalent in non-industrialized countries (Adebajo, 1997; Clark, Al-Yaman, Cowden, & Rockett, 1996; Strachan, 1989). The SAT cannot explain why autoimmune diseases are present (and show a female bias) in industrialized populations but not non-industrialized populations. Unlike the SAT, the pregnancy compensation hypothesis (Natri et al., 2019) can explain the differences in the incidence of autoimmune diseases for women in industrial versus non-industrialized nations. The pregnancy compensation hypothesis (Natri et al., 2019) suggests that differences in the prevalence of autoimmune diseases between industrialized and non-industrialized populations are because of ancestral women's immune system evolving to expect to frequently, and shortly after puberty, host a genetically distinct placenta and fetus during pregnancy without rejecting it, while simultaneously protecting the mother from pathogens and parasites. In the absence of frequent pregnancy, or by postponing pregnancy well beyond puberty, women's immune systems are proposed to experience dysregulation, with the resources that would be directed at tolerating a placenta and fetus redirected such that the immune system attacks healthy tissue.

Ancestral women were more likely to give birth closer to the onset of puberty than women are today, but even today women in industrialized nations have a longer delay between menarche and first pregnancy than women in non-industrialized nations. In 2019, the adolescent fertility rate in the United States and the United Kingdom was 17 and 12 per 1,000 women, respectively (United Nations Population Division, 2021), whereas it was 155 per 1,000 in Chad, 180 in Niger, and 165 in Mali (The World Bank, 2022), three of the least developed countries in the world (United Nations Conference on Trade and Development, 2022). Further, in the United States, the average age of a women's first pregnancy in 2014 was 26 years old, up from 21 years old in 1972 (Mathews & Hamilton, 2016), which is older than women in non-industrialized nations, like Bangladesh (Bongaarts & Blanc, 2015), and Niger (Pariona, 2017) where the average age of first pregnancy is about 18 years old, and among the Tsimane Amerindians of Bolivia, where the average age of first pregnancy is 18 (Gurven, 2012).

Second, counter to the SAT, in industrialized populations where there is evidence of a higher immune response in women than men, autoimmune disease results in significantly higher morbidity in women with autoimmune diseases, and even higher mortality in women than men (as in the case of Alzheimer's disease). The authors argue that heightened risk for autoimmune disorders observed among women is consistent with SAT, in that this is one expression of women's heightened reaction to physical threats. This argument is aligned with the health-survival paradox, also described in the paper, which states that the greater incidence of illness and severity of physical symptoms is offset by the survival enhancing benefits of a strengthened (if overly active) immune response. However, the argument that a greater prevalence of autoimmune disorders supports greater reproductive fitness among women rests on the assumption that autoimmune disorders do not reduce women's fertility. Yet, it is widely acknowledged that autoimmune disorders are associated with an increased risk for miscarriage (Gleicher, Weghofer, & Barad, 2012), and there is also evidence to suggest that autoimmune disorders reduce fecundity among women, two outcomes that would reduce reproductive fitness. Moreover, autoimmunity is associated with elevated risk for numerous infertility-linked disorders, including endometriosis, premature ovarian failure, and polycystic ovary syndrome, among other conditions (as reviewed by Haller-Kikkatalo, Salumets, & Uibo, 2012). Thus, while it may be true that enhanced survival after reproductive age could increase reproductive fitness by providing opportunities for caregiving investments to be made in older adulthood, reductions in reproductive fitness owing to increased susceptibility to autoimmune disorders would likely outweigh these benefits.

In sum, if the SAT was an evolved process for women, as explained and extended in the target article, it would not differentially impact women based on whether they are in an industrialized versus non-industrialized nation and it would not negatively impact the reproductive success of women through the increased incidence of autoimmune diseases. The sex differences in immune function, the significant increase in autoimmune diseases in women in industrialized populations, and the unique evolution of the sex chromosomes, instead, can all be explained by the pregnancy compensation hypothesis (Natri et al., 2019).

Financial support. Melissa A. Wilson was supported by R35GM124827.

Conflict of interest. None.

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The "staying alive" theory reinforces stereotypes and shows women's lower quality of life

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doi:10.1017/S0140525X22000395, e146

Abstract

Staying alive theory explains why women have more effective self-protective mechanisms in terms of woman's role as a mother and caregiver. This theory reinforces stereotypes and the relationship of oppression and submission to men. Somewhat paradoxically, it also points to women's lower quality of life, which may be explained by their greater fear of threats caused by men's power.

The "staying alive" theory (SAT) has the potential to reinforce stereotypes, not erase them, contrary to what the authors suggest. It preserves old-fashioned notions about women and ties them to their supposed subordination to raising children. If we take the perspective of a feminist philosophy that assumes that certain psychological and behavioral traits that we more often attribute to women have social rather than biological roots (Mikkola, 2017), the SAT then becomes an example of essentialist thinking about women that we should move away from. After all, it may be that women exhibit certain behaviors more frequently solely because they have been forced to do so as a result of centuries of oppression and domination by men (women as victims of violence, rape, exploitation, abuse by men [the problem of power, oppression, and discrimination in feminist ethics, see Lindemann, 2019]). Thus, an unjust social arrangement has generated the regularities described by SAT. The SAT excludes this possibility by equating the woman with the mother at the starting point.

Needless to say, this theory completely excludes not only the dynamics of homosexual couples – if we already want to remain in these exclusionary structures based on the category of relationship – but all persons other than men and women. The SAT reinforces the stereotypical role of women as caretaker mothers, emphasizing the importance of a woman's survival rate for raising offspring. This supposed biological regularity is the reason for the exploitation of millions of women around the world not only in the domestic and family circle, but also as caregivers in various areas of social life. Gender is reinforced and constituted through the repetition of gender-coded acts (Butler, 1990).

Essentialism is also evident in the philosophy of biology adopted here, which seems to assume sex differences between men and women as fundamental, fixed differences that determine the described patterns of behavior different for both sexes (Weaver & Fehr, 2017). The association of men with risky and aggressive behaviors and women with caring, aloof, and cautious behaviors may promote the reinforcement of stereotypes. An example of a stereotypical attitude is the very fact that the research and analysis are directed at inter-gender differences and the very identification of "woman" as a special, separate research category, as if it were implicitly assumed that the category "woman" is separate from the category "man" and as such, must lead to separate conclusions, because it is probably also governed by separate laws inherent only in this category. And what is the reason for the distinctiveness of these categories and the differences in the laws governing them? From differences in biology.

Although the authors cite the so-called "trauma hypothesis" as a potential alternative explanation, they reject it because, in their view, the veracity of this hypothesis should suggest the existence of stronger self-protective mechanisms in men than in women. Feminist ethics, however, points out that while men may indeed be at greater risk of death and injury from risky behavior or participation in conflict, it was men, not women, who for centuries created and developed the model of dominance and power that prevails to this day and which favors men over women. The starting point for drawing conclusions should therefore not be lethal threats, but the exploitation and subordination of women to men as the real source of self-defense mechanisms. These are incomparable types of risks.

The women's research methodology assumed by the SAT assumes a dominance relationship, or at least creates the illusion that women function within an environment that is the result of structures based on a dominance relationship (Weaver & Fehr, 2017).

It is also worth noting another SAT conclusion that is as paradoxical as it is alarming. Women have greater chances of survival and longer life expectancy, but lower quality of life by more often experiencing fear and pain, as well as more often finding themselves in social roles that cause discomfort. This conclusion, while arguably correct from a biological, medical, and psychological perspective, surprisingly conflicts with a philosophical tradition that emphasizes the importance of well-being, the so-called life worth living. The SAT shows that women inherently have lives less worth living than men, a paradoxical adaptation as long as we value quality of life rather than existence itself. This seemingly more advantageous situation for men as measured by a higher degree of well-being can be compared to Parfit's (1984) famous thought experiment about hypothetical future humans who live a life worth living for 40 years, then die as a result of radioactive waste stored by an earlier generation. But before they die, they do quite well.

It can be assumed that women's lower quality of life (living in constant stress and fear of men's aggression, threat of rape, exploitation, exclusion that makes it difficult to obtain satisfying social roles, hence more frequent depression and suicide attempts) results precisely from centuries of oppression and domination by men, and thus from a pathological social system. From this point of view, longer survival becomes a dubious advantage, further reinforcing the dominant position of men, who are freed from the possible "duty" of caring for offspring by longer-lived women who live longer precisely to care for offspring. This reinforces the feminist diagnosis of social relations in which men, even if they live shorter lives, simply enjoy life more than women who are constantly concerned about themselves and their offspring. The authors do not explain causation, but references to similar regularities in other species suggest that they recognize a biological, rather than environmental, determination of regularities such as greater concern for offspring in females than in males.

In sum, the SAT contains too many references to biological determinants, overemphasizes a woman's biological role as mother, and exposes a woman's greater responsibility and concern for her offspring. All of these are precisely the contexts in which women have traditionally been entangled and which are often used to justify the exploitation and subordination of women in their traditional roles as mothers and caregivers.

Financial support. The work on this text was written under the Bekker Fellowship (3rd edition) funded by the National Agency for Academic Exchange (Decision No. PPN/BEK/2020/1/00012/DEC/1) for a research stay at Yale University (USA) in the academic year 2021/2022.

Conflict of interest. None.

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Psychological and behavioral implications of self-protection and self-enhancement

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doi:10.1017/S0140525X22000632, e147

Abstract

Self-protection can have psychological and behavioral implications. We contrast them with the implications of a self-enhancement strategy. Both self-enhancement and self-protection have costs and benefits as survival strategies, and we identify some of the emotional, cognitive, and behavioral tradeoffs associated with the differential preferences for each strategy. New analyses on a large existing data set confirm the target article's hypothesis that women are more attuned than men to potential negative consequences of innovations.

Benenson et al. (this issue) did a commendable job of establishing self-protection as a general biological strategy that women adopt and of elucidating the strategy's health benefits (and occasional costs). They had less space for discussing behavioral implications. We assume the behavioral benefits are easy to understand, but are there hidden costs? These could indicate vulnerabilities or problems that could afflict women.

Some of our own work has explored tradeoffs between self-protection and self-enhancement (Alicke & Sedikides, 2009; Baumeister, Tice, & Hutton, 1989; Tice, 1991). Self-protection is centrally about avoiding risk. But great achievements often require risk, indeed sometimes substantial risks. A self-protective orientation can prevent disastrous failures – but may well also prevent breakthrough successes. Arguably, throughout the history of civilization, men have been responsible for the majority of both, likely driven in part by the male quest for self-enhancement. The self-protective element of female psychology may be a reason for this gender disparity.

Self-enhancement, on the other hand, is centrally about taking risks. Self-enhancement facilitates achievement (Sedikides, 2020). It is positively related to or increases the pursuit and attainment of personally important goals, while augmenting creativity. And it is linked to seeking leadership positions and being elected as a leader.

By coincidence, one of us recently participated in an investigation in which participants predicted the consequences of various hypothetical innovations (e.g., a robot to chop down trees, a procedure for cloning house pets) on a scale from −100 (mostly negative) to +100 (mostly positive) (Reece, Eubanks, Liebscher, & Baumeister, 2022). Gender was not in the study design, but demographic data were collected, thereby enabling exploratory *post hoc* reanalyses. Across all studies and conditions ($N = 1{,}567$), the male mean of 25.0 was much more positive than the female mean of 0.75. The male confidence interval was far above the neutral midpoint (zero) whereas the female confidence interval included it. Put another way, exploratory reanalyses of an existing data set found that men predicted more positive than negative consequences whereas women predicted equal amounts of both. Thus, consistent with Benenson et al.'s (this issue) theory, the potential downside of various innovations was more salient to the women than the men.

Self-enhancement has also implications for psychological health. It is associated with, predicts, and increases self-esteem (Sedikides, Gaertner, & Cai, 2015). In addition, it is positively associated with, and predicts, high levels of life satisfaction or positive affect, and low levels of negative affect or depression (Dufner, Gebauer, Sedikides, & Denissen, 2019). Moreover, self-enhancement increases life satisfaction and subjective well-being, and decreases depression, anxiety, and stress (O'Mara, Gaertner, Sedikides, Zhou, & Liu, 2012). These benefits of self-enhancement are observed across cultures.

Women report lower levels of self-enhancement (Grijalva et al., 2015) and self-esteem (Kling, Hyde, Showers, & Buswell, 1999). Further, women report lower life satisfaction and more negative affect than men, while the evidence on positive affect is inconclusive (Batz-Barbarich, Tay, Kuykendall, & Cheung, 2018). Average happiness levels across female populations are likely reduced by their considerably higher incidence of depression (Salk, Hyde, & Abramson, 2017). Benenson et al. (this issue) note the link between female self-protection and depression but do not offer much explanation other than the heightened sensitivity to pain. There may be multiple links, including the lesser use of self-enhancement.

Another traditional theme of gender theory is the tradeoff between agency and communion (Bakan, 1966), with women being less agentic but more communal than men (Hsu, Badura, Newman, & Speach, 2021). This too fits well into the self-protection analysis. Agency means taking initiative, which brings risk. Communion means connecting with others, which is vital for safety. The female self-protective orientation would plausibly contribute to a shift in their psychology toward greater communion rather than agency. Again, the benefits from such a shift are clear, but the lesser agency might carry costs such as lesser achievement or innovation.

A related pattern emerges from clinical observations. People adopt self-protective patterns or schemas during difficult childhood or adolescent periods, and then sometimes maintain these in adult relationships. These schemas have high predictive value by repeating the same feelings or experiences over and over again. If men engage in this practice, women engage in it more (Shorey et al., 2012). These schemas generate high levels of negative affect and self-defeating consequences, and go against self-enhancement (Young, Klosko, & Weishaar, 2003).

In closing, we concur with Benenson et al.'s (this issue) powerfully integrative idea that women tend to adopt self-protection as a general strategy. This strategy has certain advantages, which could be complemented by a trade-off with a self-enhancement strategy.

Financial support. The authors declare the received no outside financial support for this work.

Conflict of interest. The authors declare no financial interest.

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Women amid the COVID-19 pandemic: Self-protection through the behavioral immune system

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doi:10.1017/S0140525X22000413, e148

Abstract

Studies of the activation of the behavioral immune system triggered by the coronavirus disease-2019 pandemic have demonstrated that evolutionary explanations of individual differences in self-protection should not be based only on parental investment and sexual selection theory. An evolutionary model must also incorporate individual differences that arise within each sex as a result of life history strategies and attachment patterns.

The coronavirus disease-2019 pandemic presents a unique opportunity to test the evolutionary hypothesis that women show stronger self-protective reactions than men to environmental threats. In their target article, Benenson et al. focus mainly on sex differences in COVID-19 mortality rates and the activation of the physiological immune system. Their argument can be expanded by analyzing sex differences in the activation of the behavioral immune system and women's emotional reactions to the risk of COVID-19 infection.

The physiological immune defense is merely reactive because it is triggered only after the infection has occurred within the body. Schaller (2011) has convincingly demonstrated that selection pressures have reinforced our defenses against infections by causing the evolution of a behavioral immune system that is separate from, and complementary to, the physiological immune system. The behavioral immune system includes a set of proactive mechanisms that inhibit contact with pathogens in the first place. These mechanisms offer a sort of psychological and behavioral prophylaxis against infection. The two emotional and interrelated reactions associated with the activation of the behavioral immune system are fear of infection and pathogen disgust sensitivity (Troisi, 2020). Based on the evolutionary hypothesis of sex differences in self-protection, the COVID-19 pandemic is expected to have caused more intense fear of infection and pathogen disgust sensitivity in women than in men.

Data on fear of infection support the evolutionary hypothesis. A recent scoping review based on 14 studies conducted in different populations showed that female gender was the most consistent predictor of fear of COVID-19 (Quadros, Garg, Ranjan, Vijayasarathi, & Mamun, 2021). Compared to studies focusing on fear of infection, reports on sex differences in disgust sensitivity are fewer but their findings are anyway consistent with evolutionary predictions. Using a large nationwide Chinese sample, Ding, Yang, Ji, and Guo (2021) found that the COVID-19 outbreak increased levels of pathogen disgust sensitivity more in women than in men. In a large sample of Australian university students, Stevenson, Saluja, and Case (2021) found that the increase in disgust sensitivity observed during the COVID-19 pandemic was significantly greater in women than in men.

The COVID-19 outbreak is a natural experiment that not only confirms the existence of sex differences in self-protective reactions to environmental threats but also enriches our understanding of their evolutionary-developmental origin. Studies of the activation of the behavioral immune system triggered by the COVID-19 pandemic have demonstrated that evolutionary explanations of individual differences in self-protection should not be based only on parental investment and sexual selection theory, as Benenson et al. have done in their target article. A comprehensive evolutionary model of greater or lower levels of self-protection must also incorporate the individual differences that arise within each sex as a result of life history strategies and attachment patterns.

Life history theory is a mid-level evolutionary framework that explains individual differences in a variety of interrelated phenotypic traits including physiology, psychology, and behavior. At the core of the life history theory is the appreciation for the long-lasting influence of ecological information acquired in early development being utilized as a forecast in service of meeting the environmental demands of later development. Individual variation in life history strategies (i.e., different patterns of allocation of finite time and energy budgets between competing activities) can be arranged along a continuum, from "fast" to "slow" (Del Giudice, 2009). In terms of psychological attitudes and behaviors related to self-protection, slow strategists are characterized by higher levels of harm avoidance and risk averseness. Fast strategists are characterized by the opposite pattern, showing higher propensity toward impulsivity, short-term planning, and risk taking. Using an online survey tool, Corpuz, D'Alessandro, Adeyemo, Jankowski, and Kandalaft (2020) found that, among 209 U.S. adult participants interviewed during the first wave of the COVID-19 pandemic, life history orientation predicted endorsement of precautionary measures. Compared to fast strategists, slow strategists endorsed higher levels of self-protection (e.g., wearing a mask or to stay-at-home).

The attachment system is an important psychological mechanism that bridges the gap between early exposure to environmental harshness and/or unpredictability and life-history strategies enacted in adulthood (Szepsenwol & Simpson, 2019). Different attachment patterns (secure, preoccupied, fearful, avoidant) exert major effects on emotion regulation and, therefore, they are likely to impact individual attitudes toward self-protection. In line with such a prediction, in a sample of 101 Italian healthcare workers employed in a COVID-19 university hospital, Troisi, Croce Nanni, Riconi, Carola, and Di Cave (2021) found that participants with higher levels of fearful attachment reported more intense fear of infection.

Interestingly, neither the study by Corpuz et al. (2020) nor the study by Troisi et al. (2021) found significant relationships between sex and the dependent variables reflecting individual attitudes toward self-protection. These findings do not necessarily mean that the evolutionary hypothesis advanced by Benenson et al. in their target article is invalid. Rather, they suggest the necessity of integrating the predictions derived by asymmetrical parental investment and sexual selection theory with those based on life history theory and attachment models. Given its importance for survival and biological adaptation, the evolution of the behavioral immune system is likely to have been shaped by multiple selection pressures. A comprehensive understanding of the psychological and behavioral defenses against infection requires a conceptual framework that integrates different evolutionary subtheories: parental investment, sexual selection, life history strategies, and attachment orientations. The COVID-19 outbreak offers a unique opportunity to apply such an integrated framework to the study of self-protective behavior.

Financial support. This research received no specific grant from any funding agency, commercial, or not-for-profit sectors.

Conflict of interest. None.

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Pathological complexity and the evolution of sex differences

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doi:10.1017/S0140525X22000498, e149

Abstract

Benenson et al. provide a compelling case for treating greater investment into self-protection among females as an adaptive strategy. Here, we wish to expand their proposed adaptive explanation by placing it squarely in modern state-based and behavioural life-history theory, drawing on Veit's *pathological complexity* framework. This allows us to make sense of alternative "lifestyle" strategies, rather than pathologizing them.

Benenson, Webb, and Wrangham (2022) provide an excellent empirical synthesis of data from different fields to support the idea that a greater investment into self-protection has evolved as a unique adaptive strategy in females. They draw on data that provide varying levels of support for the hypothesis that human females do produce stronger self-protective reactions than males, to a range of threats, which then suggests the presence of a general female self-protection strategy that may be adaptive rather than pathological. Nevertheless, the question then remains as to how best explain the results, and identify the adaptive function of domain-general self-protective behaviour. The authors locate this within Campbell's "staying alive" theory: That human females have a higher fitness value arising from self-protection than males do.

Here, we wish to expand their proposal by placing it squarely in modern state-based and behavioural life-history theory, which – despite a brief mention – was surprisingly not discussed within the target article. Life-history theory originated in simple models representing the necessity of a trade-off between longevity and the number of offspring created in a particular breeding period to maximize fitness (Stearns, 1992). Even this restricted approach to modelling life histories has demonstrated that greater offspring care leads to an investment into survival, rather than reproductive output (Hamilton, 1966; Williams, 1966). While Benenson et al. mention this part of the literature, they do not draw on the subsequent extension of this early work, which proceeded through the inclusion of behaviour and varying bodily states, to eventually lead to state-based behavioural and life-history theory (McNamara & Houston, 1996). This theory is not only important to understand the ecological lifestyles of different species, but also to assess the *teleonomic* complexity of different organisms in achieving their goal of reproduction – or rather, fitness-maximization – as it is only within such an ecological theory of the organism that we can distinguish pathological traits and behaviours from adaptive ones.

It is for this reason that one of us has used the term "pathological complexity" to refer to the complexity of this set of trade-offs, that is, the number of parameters and constraints in the teleonomic optimization problem, studied by modern state-based behavioural and life-history theory (see Veit, 2022a, 2022b). The term "pathological" here is not meant to imply that life-history complexity is inherently pathological; but rather that it is only in assessing this complexity of optimizing trade-offs to maximize fitness that we can determine which behaviours are pathological. This can be done by calculating the trade-offs inherent to different life-history strategies, with fitness serving as the common currency of organismal design, which a common example within life-history theory will help to illustrate. In Australian marsupials of the genus *Antechinus*, males typically die after a single breeding season. While such behaviour in males may be seen as strikingly pathological, through life-history theory we can see that it is not. Their best response to their species-specific pathological complexity is to invest all their resources into reproduction in a single breeding season, and hence this is not pathological.

Some life-history strategies will have higher pathological complexity than others, due to the higher number of parameters and constraints in their environment and evolutionary design. Again, this does not make their responses pathological, but it makes their design a more complex trade-off problem to be solved. If a life-history strategy puts all efforts into reproduction in a single period, there will inevitably be fewer complex trade-offs to be solved. Indeed, pathological complexity can be increased through external factors (e.g., the presence of predators) or internal ones (e.g., the need for a greater variety of nutrients), as well as the availability of more degrees of freedom of behaviour, which can greatly increase the computational problem of maximizing fitness both for the organism and for those modelling their life-history strategies. If we fail to account for one of those factors in our models, we will inevitably come to re-examine mistaken evaluations of some behaviours as pathological when we gain a greater understanding of species- and sex-specific life-history strategies.

It is thus hardly surprising that we urge the use of life-history theory in answering the question of whether females have a different optimal design solution to deal with their particular pathological complexity arising from the trade-off between survival and reproduction. It is *the* framework to assess the adaptive nature of diverse female traits and to challenge prevailing ideas about the pathological nature of differences between the sexes. In order to evaluate whether self-protection is sex-specific, life-history strategy requires investigation into the different social and ecological niches faced by human males and females, both currently and throughout our adaptive history, to identify possible factors – or sets of factors – that could serve to explain the observed difference in behaviour. For instance, it is possible that females face a greater range of potential threats to survival and reproduction, and hence require a more complex adaptive behavioural phenotype in response. If survival is more important for females than it is for human males, this may well suggest that their life-history complexity is higher with more threats to keep track of – demanding unique and more risk-averse adaptations, just as the authors suggest.

Finally, we applaud the application of this work, in demonstrating that the distinctive female responses to threat are an adaptive reaction to their differential niche, and should thus not be pathologized. For too long, deviations from the male "norm" have been seen as problematic, rather than simply different acceptable strategies. As the authors suggest, this can enhance understanding of female health and well-being with reference to what is normal for this group. Experiences and conditions that are more common in females – such as pain disorders, anxiety, and autoimmune diseases – can be examined and treated accordingly. A deeper understanding of the environmental challenges that have shaped these sex differences, and where they currently still do or do not apply, could also assist in determining when there is a normal reaction or a pathological maladaptation to modern social and living conditions.

Financial support. WV's research was supported under Australian Research Council's Discovery Projects funding scheme (project number FL170100160).

Conflict of interest. The authors have no conflicts of interest to report.

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Sex differences in longevity are relative, not independent

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doi:10.1017/S0140525X22000401, e150

Abstract

I ask three questions related to the claims made within the staying alive theory (SAT): Is survival more fitness-enhancing for females than for males? Does the historical record on sex differences in mortality support the SAT? Is it possible to talk about "independent selective pressures on both male and female traits" when all we have are sex/gender comparisons?

A central tenet of the target paper is that "survival is more fitness-enhancing for females than for males." There is something odd about this claim, since survival is a necessary condition for reproductive fitness. Without survival there is no reproduction. Without further specification it thus becomes meaningless to talk about sex-differences in fitness linked to survival. A favorable reading of the paper says that the authors are really aiming not at survival but longevity. In other words: survival beyond a certain point. One crucial time point is obviously mating. Before mating survival is infinitely fitness-enhancing for both sexes.

Beyond mating, the mother's reproductive fitness relies on her survival during pregnancy as well and this is where the paths of the two sexes diverge. The fitness of the father no longer depends on his own survival, but solely on the survival of the mother and the fetus. One may therefore argue that after this time point there is a stronger evolutionary pressure on the survival of the mother than on the father. After the child is born, the reproductive fitness of both parents depends on the survival of the child. The authors convincingly argue that mothers spend more time than fathers looking after their children and that her survival thus may be more important for the survival of the child than that of the father. This seems to be the evolutionary account behind females' longer life expectancies, according to the staying alive theory (SAT). However, it misses one crucial point. Males are fertile throughout their lives, and their fitness is not tied to one individual pregnancy. It is therefore difficult to see why longevity would not also increase male fitness equally, given that longer life would provide opportunities for additional mating. Data exist to support a correlation between parity (i.e., reproductive fitness) and longevity in both sexes (Barclay & Kolk, 2019; McArdle et al., 2006). Within this naive evolutionary framework for human reproduction, which disregards culture, family, and parental collaboration, longevity thus appears to be an advantage for both sexes. More effort is needed to flesh out why the evolutionary advantage of longevity would be greater for females than for males.

Does the historical record on sex differences in mortality support the SAT? Following the link to parental care, the authors predict "increased magnitudes of sex differences following puberty." However, when making a detailed investigation of differences in mortality, the picture is not clear. Excess male deaths in reproductive years (between 15 and 40), where the evolutionary pressure would occur according to the SAT, account for less than 25% of the life expectancy gap, both presently and historically (Zarulli, Kashnitsky, & Vaupel, 2021). The sex difference in life expectancy is also to some extent a recent phenomenon (Beltrán-Sánchez, Finch, & Crimmins, 2015; Thorslund, Wastesson, Agahi, Lagergren, & Parker, 2013; Wilmoth, 2007). The growth of the gap in mortality in the twentieth century (Fig. 1) can to a large extent be explained by differences in smoking habits (Preston & Wang, 2006) and lung cancer is still one of the most significant predictors of sex differences in age of death (main article, Fig. 2). However, historically, most excess male death occurred during the pre-mating stage of life (0–14 years) (Zarulli et al., 2021), with infant deaths carrying the majority of the burden (Fig. 1). Doesn't both the historical variability of sex/gender differences in life expectancy and the changing distribution of excess deaths in males across age-spans yield an explanatory challenge for the SAT which proposes that the difference is due to an independently adapted female trait linked to "parental investment"?

Furthermore, is it possible to talk about "Independent selective pressures on both male and female traits" when all we have are sex/gender comparisons? The claim in SAT that lower levels of aggression forms "a positive female adaptation driven by the critical importance of the mother's survival for her own reproductive success" (Campbell, 1999) has an important flaw. If less is more, then having nothing may be even better. One could argue that not having antlers or peacock feathers are positive

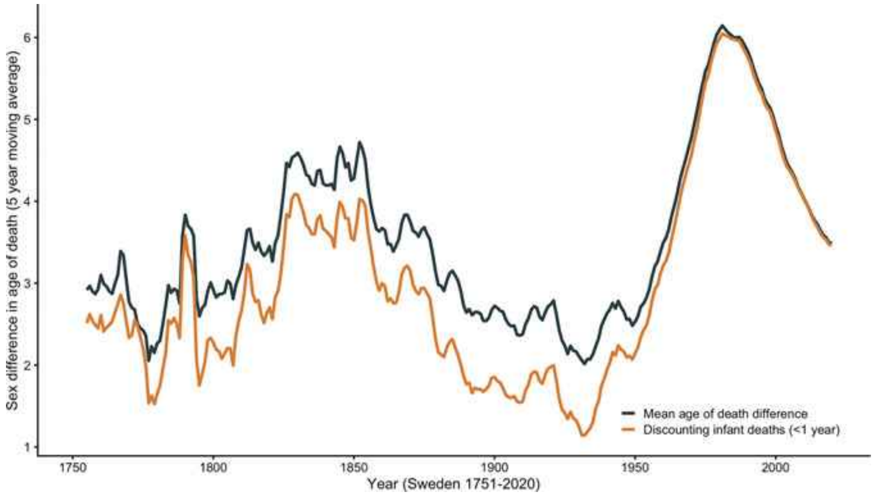

Figure 1 (Wallentin). Differences in average age of death across time (moving average 5 years) when including or discounting infant deaths. The difference in life expectancy has varied through history, and much can been explained by differences in infant mortality. Data from Sweden, adapted from the Human Mortality Database (mortality.org).

female adaptations. There is an infinite list of such adaptive lack of properties within this type of logic. It is therefore vital to focus on actual positive attributes and behaviors. This, however, rests on the assumption of independence. In the conclusion, the authors state that "independent consideration of each sex, along separate dimensions, is necessary for understanding the ways in which each sex's traits are optimized." Specific male traits are argued to include: "direct competition, physical aggression, risk-taking, showing off, impulsivity, sensation-seeking, and resource accumulation." The SAT, on the other hand, advocates that "females more than males evolved to avoid physical aggression." It is not difficult to see that this is just a reversal of what is reported as a male adaptation. The critical claim "that lower rates of aggression by women reflect not just the absence of male risk-taking but are part of a positive female adaptation" remains untested and perhaps untestable in a binary comparison between males and females with only one effective degree of freedom. Thus, in the conclusion the authors state that "Had the evidence existed, we would have compared the reproductive success of females who varied in their degree of reactions to threats, and not included males at all." Are the authors willing to stick their neck out and hypothesize that females who adhere to the description in their paper, that is, are more pain sensitive, who wake up at night, are more fearful and neurotic, also live longer and have greater reproductive success than females who do not? If so, would one end of the spectrum be less female than the other? Would that make the outcome independent?

Financial support. This study was supported by Independent Research Fund Denmark grant 0132-00081B.

Conflict of interest. The author has no conflicts of interest to declare.

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Authors' Response

Females undergo selection too

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doi:10.1017/S0140525X22000644, e151

Abstract

Extending Campbell's (1999) staying alive theory (SAT) beyond aggression, we reviewed evidence that females are more self-protective than males. Many commentators provided additional supporting data. Sex differences in life-history adaptations, in the optimal relation between survival and reproduction, and in the mechanisms underlying trade-offs involved with self-protection remain important topics with numerous opportunities for improved understanding.

We very much appreciate the thoughtfulness and insights of the commentators. A number of commentators contributed novel evidence and ideas that expanded staying alive theory (SAT) and provided new directions for future research. Others questioned whether sex differences exist in the value of survival for fitness. A third group believes that the evolution of male mate competition rather than any female adaptations for longevity explain sex differences in self-protectiveness. Finally, a few questioned whether a biological/evolutionary basis for sex differences is a viable or useful consideration in analyses of human beings. We consider each of these in turn.

R1. Additional evidence and future directions

Both **Hawkes** and **Veit and Browning** expand SAT by using life-history theory to understand whether females approach the trade-off between survival and reproduction differently than males do. Much of Campbell's SAT and our extension of it is derived from or consistent with Hawkes' research demonstrating that women enhance the reproductive success of both their offspring and their grandchildren. While a former idea that only males can benefit by extending their reproductive careers into old age is therefore wrong, Hawkes nevertheless emphasizes that precisely how the reproductive strategies of each sex are expected to differ remains a complex problem. Her analyses of the trade-offs between survival and reproductive success for each sex provide avenues for future research, including in terms of understanding residual reproductive value, mating sex ratios, birth spacing, and grandmothering.

We appreciate **Veit and Browning**'s focus on the importance of carefully weighing whether commonly occurring, cross-culturally present patterns of behavior, such as those we have identified in girls and women, should be dubbed "pathological." What looks pathological from one perspective may be adaptive from another. Veit and Browning suggest that further research is needed to investigate whether compared to males, females face more threats, find modern life more difficult, or need to live longer to be reproductively successful. We have focused on the latter as a reason for females' greater reactions to threat. Nonetheless, we fully concur that more focus on the details of females' and males' life histories and the components that may maximize reproductive success (RS) for each sex are necessary in order to distinguish pathology from normality.

Bleske-Rechek and Deaner add the important insight that cultures often prioritize the survival of females over males. Their evidence is compelling that in times of disasters, in the military, or in dangerous jobs more generally, females' lives are prized over males' lives at least in many western, educated, industrialized, rich, and democratic (WEIRD) societies. Furthermore, women are more likely than men to be perceived as victims and female victims generate more sympathy than male victims. Their evidence added to the SAT suggests that a biological basis for females' greater self-protectiveness is complemented by widespread social norms stipulating that females merit greater protection than males. Further investigation across non-WEIRD cultures could help verify the universality of this norm.

The coronavirus disease-2019 (COVID-19) data presented by **Troisi** perfectly fit the predictions of SAT. Referring to the importance of the behavioral immune system, Troisi presents evidence that women are more fearful than men of contracting COVID-19 and exhibit a larger increase than men in disgust sensitivity to pathogens. Nevertheless, he argues, and we agree, that many other factors besides sex are important in determining how the behavioral immune system functions. Two factors in particular, slow versus fast life histories and fearful versus not fearful attachment patterns, were shown by Troisi to affect the behavioral immune system's reactions to COVID-19. Although those factors were unrelated to sex, it would be interesting to investigate whether more males than females opt for a faster life history (Del Giudice, 2009) or begin life with disorganized/fearful attachments (Carlson, Cicchetti, Barnett, & Braunwald, 1989) as some have suggested, which could influence the interaction between sex and these variables.

We appreciate the evidence that **Tice, Baumeister, and Sedikides** (**Tice et al.**) provide from a re-analysis of their data that elegantly fits predictions from SAT. Their results show that females are much less enthusiastic than males about potentially dangerous hypothetical new inventions, such as a tree-chopping robot or a pet cloner. They concur that females are more self-protective than males, but they add that this can entail costs. Specifically, they hypothesize that greater self-protectiveness reduces self-enhancement, which is associated with greater life satisfaction, higher self-esteem, more positive affect, and lower levels of anxiety and depression. Thus, they postulate that anxiety and depression in particular can be multi-determined, caused by both extreme forms of self-protection and/or reduced levels of self-enhancement. Worldwide however, no evidence shows that females exhibit lower life-satisfaction or less positive affect than males, and if anything females appear more positive (Bem, 1974; Lucas & Gohm, 2000). Furthermore, cross-culturally sex differences in anxiety and depression along with many of the other self-protective characteristics we have described, such as insomnia, smiling, or neuroticism, emerge or are accentuated in puberty. It seems unlikely that sex differences in self-enhancement suddenly emerge in puberty. Nonetheless, we concur that self-protection likely inflicts costs as Tice et al. propose, which may be related to reduced self-enhancement depending on its definition in a particular culture. SAT posits that for females the costs of self-protection are outweighed by the benefits of enhanced survival of themselves and their descendants.

March and Gaertner distinguish between detection of and reaction to visual threat. We appreciate their re-analysis of their data to show that females exhibit stronger reactions than males specifically to threatening stimuli as would be predicted by SAT. What females do not exhibit however is faster detection of threat which also would be expected by SAT. This disparity is intriguing and warrants further investigation. One possibility is that it depends on sex differences in visual acuity. Although the cause is not genetic, myopia is twice as prevalent in white and East Asian females as males by late adolescence according to a large meta-analysis (Rudnicka et al., 2016). In contrast, much evidence supports the lower threshold of females than males for detecting varied types of auditory, olfactory, and tactile stimuli (Velle, 1987). Further research is necessary to examine whether females would detect threatening stimuli more rapidly than males using other sensory modalities.

Cassar adds to our conceptualization of the social relations that would be predicted by SAT. She suggests that reducing competition benefits females not only through harm avoidance and protection of relationships but also by facilitating future cooperation. Her thesis is that cross-culturally females tend to display more egalitarian behavior than males in order to buttress reciprocal relationships with unrelated females and asymmetrical relations with higher-ranked mates. By insisting on equality, females signal that they are not planning to compete directly against another female or a mate. Nonetheless, as Cassar has shown, females will compete under some contexts, such as in support of their own children or on others' behalf, ways of competition that may be acceptable to unrelated females and a mate. Emphasizing equality or competition for acceptable outcomes therefore reduces threat, which would be in line with SAT.

Crosby, Hahnel-Peeters, and Buss (**Crosby et al.**) and **McDonald and James** note that we omitted processes directly related to females' and males' unique concerns about reproduction. Thus, morbidity or mortality related to childbirth, gestation, and lactation; female or male reproductive organs; and sexuality were excluded. Our purpose was to compare processes that could threaten females and males to the same extent.

As **Crosby et al.** highlight, sex differences in self-protective behavior would be even greater if some of these were included. The examples they provide demonstrate this convincingly. For instance, one of the largest sex differences occurs for sexual disgust (see also Sparks, Fessler, Chan, Ashokkumar, & Holbrook, 2018). Crosby et al. make the compelling argument that this protects women from sub-optimal mates and sexually transmitted diseases. Likewise, both **McDonald and James** and Crosby et al. emphasize that fear of rape is one major reason for women's self-protective behaviors. McDonald and James go even further and suggest that threats to survival and to reproductive choice are conflated for women and should be distinguished, especially for the social behaviors we describe. We are unsure how they could be disentangled as they are not necessarily mutually exclusive. For instance, rape can co-occur with murder. Furthermore, if fear of rape were the sole reason for the greater self-protective social behaviors exhibited by females than males, then self-protective social behaviors and neuroticism would be unnecessary with other women. This is not the case. Several of the self-protective behaviors we described, including smiling, politeness, or identification of emotions, are even stronger when girls and women interact with same-sex peers than with their male counterparts. Nevertheless, had we included all sex-biased concerns about reproduction and sexuality, then some unique aspects of male reproductive success, such as public displays of wealth, degree of sexual motivation, or erectile function, would be more threatening to males than females, unless these threatened females' lives personally.

Archer and **Fuentes** suggest that SAT would be improved by examining how self-protective characteristics co-vary and whether they form a package. As Archer recommends, using multivariate statistical analyses such as Mahalanobis's D permits examination of covariation between the characteristics we identify. We expect that covariance will be strong in human females, as many studies already demonstrate positive associations between two or more of the self-protective behaviors we have described including among immune functioning, pain, sleep, social behaviors, neuroticism, and emotional reactions to threat. If the disparate self-protective reactions form a single package, this could motivate useful ideas about underlying mechanisms.

Archer further asks how sexual selection theory and SAT fit together. We accept that sexual selection theory, which typically refers to male mate competition, is usefully redefined as natural selection that includes each sex's reproductive strategies (Carranza, 2009). This permits male mating competition, female self-protective behaviors, as well as many other sex-differentiated strategies for survival and reproductive success to be categorized under one overarching rubric (Clutton-Brock & Huchard, 2013; Stockley & Bro-Jørgensen, 2011). As **Aung, Baek, and Puts** (**Aung et al.**), **Wallentin**, and others recommend, understanding of the ultimate and proximate mechanisms that produce specific traits will be better illuminated after the differential forces that shape particular adaptations or groups of adaptations are identified. Some of these will differ by sex.

R2. Is longevity more important to females' than males' reproductive success?

Several commentators question our postulation that longevity is more important to reproductive success for females than males, including **Brooks and Blake**, **Hagen, Knorr, Li, Mensing, and Scelza (Hagen et al.)**, and **Wallentin**. Because theoretically only males can reproduce until death, common wisdom holds that survival at late ages is *less* important for females than males. SAT is constructed on the opposite premise, that extended survival is more important for the reproductive success of females than males. This analysis relies heavily on **Hawkes** and others' research on the importance of grandmothering (Campbell, 1999; Hawkes et al., 1997; Sear & Mace, 2008). Lacking the input for a mathematical or game theoretic model, we present several assumptions that support our premise.

First, *all* women benefit reproductively from staying alive long enough to invest in both children (especially daughters) and grandchildren (Daly & Perry, 2021; Hawkes et al., 1997; Sear & Mace, 2008). Second, men's fighting power (Daly & Wilson, 1988), fluid cognitive abilities (Salthouse, 1996), and fertility decline with age (Matsumoto, 2002; Santiago, Silva, Alves, Oliveira, & Fardilha, 2019), thereby reducing many elements that contribute to male mating success. Thus, in a contemporary study of over 330 million births across 17 rich European nations, where men live longer than in poorer areas, "age-specific fertility rates of men quickly decline to very low levels above age 45" (Dudel & Klüsener, 2021, p. 424). Ages 20–45 years were men's maximum reproductive years and at most 0.2% of men became fathers after age 59 years. Therefore, despite the extended reproductive success of a few famous men (Betzig, 1986), relatively few older men can amass enough resources to both outcompete younger, stronger men and be attractive to younger, fertile women. In contrast, despite large variation across 25 contemporary Western nations in when grandparenthood begins (ages 47–60), a first grandchild is born when a grandmother is on average 51 years and a grandfather is 54 years (Leopold & Skopek, 2015). Mortality in this sample is 83 years for women and 78 years for men, so that grandparenting can in theory extend for decades following the end of fertility. In a separate analysis of 12 contemporary European nations with over 36,000 grandparents older than 50 years and a grandchild younger than 13 years, grandmothers were more than twice as likely as grandfathers to provide frequent care to their biological grandchildren (Daly & Perry, 2021). Furthermore, when they helped, grandfathers invested as much in non-biological children as biological children. The mean age of grandmothers was 63 years (range 50–96 years) and grandfathers 65 years (range 50–100 years). Thus, while a few older men, particularly in polygynous societies, greatly increase their reproductive success until the end of their lives at the expense of younger men's reproductive success, most men in monogamous societies follow a similar reproductive age trajectory as women albeit beginning and ending a few years later. Furthermore, it seems unlikely that this should differ in subsistence societies where lifespan tends to be shorter.

Brooks and Blake provide several important theoretical reasons why more research is necessary to understand the relation between survival and reproductive success, especially for human females and males. They cite the aphorism that applies to many taxa that males "live fast and die young" and elaborate on how greater extrinsic mortality can act then to enhance mortality from intrinsic causes. They then make an exception for humans by suggesting that the greater survival of women over men may be incidental. As examples, because women's survival is traded off against childbirth and childcare, which increase mortality, reduced fertility in contemporary society may artificially increase women's survival. Alternatively, because amassing resources and status takes time and increases reproductive success for men as **Hagen et al.** also argue, selection for longevity may have increased for males: Increased longevity in females would then be a by-product. These are important questions, and we await further evidence. Nonetheless, worldwide across natural fertility populations in small scale societies, females live longer than males (Ember & Ember, 2003). Precise supporting data exist from Sweden from the 1700s (Allman, Rosin, Kumar, & Hasenstaub, 1998) quantifying the sex difference as **Wallentin** partially depicts in the graph he includes.

Hagen et al. concur that a mother is more important than a father to a child's survival. This might well explain what **Bleske-Rechek and Deaner** emphasize: Cultures routinely prioritize survival of women over men. Nonetheless, paternal investment can enhance RS especially when women live with their husbands' families or lack the support of female kin. Therefore, women should select husbands who will provide extended assistance or resources. Hagen et al. and **Brooks and Blake** argue that men need time to acquire lots of resources to attract women and outcompete same-age and younger men. Whether this occurs routinely in primarily monogamous societies however seems unlikely based on contemporary evidence, where women prefer mates 2–3 years older than they are (Walter et al., 2020). Thus, even though the average age of first reproduction has always been higher for males than females across primate species (Bogin, 1999) and human females undergo menopause, we postulate that on average, longevity is more important for females' than males' reproductive success.

Nevertheless, we fully acknowledge that more empirical research is required to examine the relation between longevity and reproductive success for each sex as **Brooks and Blake** recommend. A life history approach as endorsed by **Hawkes**, Brooks and Blake, and **Veit and Browning** will help clarify the trade-offs between reproduction and survival for females and mating competition and survival for males. All other things being equal, both women and men gain reproductive success from living longer, but we suggest that the marginal value is higher for women than men because of women's greater investment in children and grandchildren.

R3. Females' greater longevity: Selection for survival or incidental to males' mate competition?

Relatedly, another group of commentators argue that the sex difference in self-protectiveness results solely from a trade-off with risk-taking. **Aung et al.** and **Wallentin** are explicit that females are more self-protective than males only because males' greater mate competition prevents males from being maximally self-protective, not because of any specialized evolutionary adaptations unique to or extended in females. Likewise, in a paper of which we were formerly unaware that presents a theory and evidence that resembles our target article in many ways by Sparks et al. (2018), males' risk-taking is presented as the reason why females are more self-protective.

Campbell argued specifically against this proposition, and we quoted her statement in our target article "that lower rates of aggression by women reflect not just the absence of male risk-taking but are part of a positive female adaptation driven by the critical importance of the mother's survival for her own reproductive success" (p. 204). We extended Campbell's (1999) SAT to examine further evidence that females exhibit many adaptations that protect them from threats. Our primary point is that women who have stronger immune systems, faster withdrawal responses to potentially injurious stimuli, more awareness of nighttime and general environmental adverse forces, greater avoidance of social threats, and a healthy degree of worry and sense of vulnerability would live longer than those women who did not have these reactions, and that this would be beneficial in terms of fitness. As we described, evidence exists for female nonhumans and humans that self-protectiveness, including immunological, pain threshold, sleep cycles, and behavioral conflict avoidance, is regulated by estrogens. More generally, those individuals who respond more self-protectively to any threat will generally survive longer, and females do so more than males. If these reactions become too extreme, they become maladaptive, and they may carry costs as **Tice et al.** point out, but on balance, self-protective reactions prolong life. Critically, SAT emphasizes that females' self-protectiveness does not arise as an incidental result of males' risky mating strategies. Instead, females have evolved mechanisms that have allowed them to prolong their lives. As previously emphasized, sex differences in mortality at all ages are well-supported by the graph **Wallentin** includes from the Human Mortality Database. Infant deaths perfectly track deaths that do not include infants. Sex differences also clearly vary over time, but they are always present even in Sweden in the 1700s (Allman et al., 1998).

Wallentin further wonders what evidence indicates that it is caregiving that accounts for the benefits of greater self-protectiveness in females. Across eight species of nonhuman primates, the ratio of female to male care of offspring is positively associated with the ratio of female:male lifespan to the point that in the callitrichid *Callimico*, which has particularly extensive care by males, lifespans show no detectable sex difference (Allman et al., 1998). This example illustrates the wider point about sex differences in adaptation that we take from Campbell (1999). In species in which male–male competition is relatively worthwhile, investment in adaptations for competition is more beneficial for males than investment in longevity. Males' longevity is therefore reduced. For the females of those species, however, investment in longevity yields positive adaptive benefits. The relatively extended lifespans of females thus reflect both the absence of the trade-off faced by males and the high value of long-term survival for females.

R4. Sex is not a useful construct for understanding self-protectiveness

A final group of commentators do not believe sex contributes to understanding self-protective behaviors. In the first sub-group, **Lin, Cuijpers, and Li (Lin et al.)**, **Humeny**, and **Eagly** suggest that in some cases women are not more self-protective than men, thereby challenging the validity of SAT.

Lin et al. raise two important examples of women's appearing less self-protective than men: Burnout in response to difficulties with work–life balance and depression surrounding the birth of a child. We suggest that these challenges are more specific to or pronounced in women than in men, as with concerns raised by **Crosby et al.** and **McDonald and James**. Consequently, comparisons with men are not equivalent. Lin et al.'s examples depend on women's taking primary responsibility for raising children and thus being more affected by burnout and childbirth. For example, in a meta-analysis of reasons for female and male physicians' burnout, amount of workload, number of hours required, night-time shifts, schedule inflexibility, and lack of supportive relationships were some of the primary reasons for burnout (Azam, Khan, & Alam, 2017). Too many work demands obviously are more detrimental to primary than secondary caregivers. In turn, the causes of perinatal depression have not been well identified, with both physiological responses to pregnancy and lack of social support commonly cited (Eastwood, Kemp, & Jalaludin, 2015). Nonetheless, bearing primary responsibility for the survival of oneself and a newborn and possibly other children and family members, especially when difficulties arise, would seem to necessitate strong responses. Newer theories view these types of strong responses as ways of social bargaining (Hagen & Thornhill, 2017; Syme, Garfield, & Hagen, 2016). Recent evidence suggests that when single fathers assume full responsibility for childcare, they are three times more likely to die than partnered fathers or single mothers (Chiu et al., 2018). SAT would predict that women would respond more rapidly than men to reduce threats whether by leaving an overwhelming job faster or procuring assistance with child-rearing under difficult circumstances.

Humeny describes women who are victims of intimate partner violence as not being self-protective. Again, this predicament is not equivalent for the two sexes. Being a victim of intimate partner violence is more common and more lethal for women because they are less physically strong as we noted in our target article. As Humeny adds however, being isolated from others and alone with an abusive partner can make it very difficult for a woman to be self-protective. In particular, attempts to leave a violent partner may be less self-protective than remaining with him. Thus, women may be choosing the most self-protective behavior available by staying with an abusive partner, especially if no one else will protect them. We find it difficult to view severe victimization from which there is little escape as evidence against women's motivation to protect themselves, despite the fact that abuse inflicts serious physical and emotional damage.

Eagly provides three further important examples in which women are less likely than men to protect themselves. First, women more than men donate their kidneys, which incurs risk. Second, more single German women than single men protected Jews during the holocaust. Third, more women than men join the Peace Corps which often entails traveling to and living in areas with greater health risks. We agree that these examples raise important questions that merit consideration. For instance, how many of the organ donations are to kin? And when women take explicit risks, what are their male counterparts doing? As Eagly notes, women have always been less likely than men to enter life-threatening professions from fighting fires, to policing, to responding to natural disasters, as well as engaging in social conflicts including the military, showing off, driving recklessly, and so forth. Thus, it is plausible that during the holocaust, for example, men engaged in even more dangerous enterprises than women. Accepting Eagly's data however, all else being equal, SAT predicts that these women who purposefully place themselves in danger by definition would have a lower probability of survival and reproductive success than women who choose not to engage in dangerous activities and thus would represent exceptions. Without knowing the specific circumstances of each woman who purposefully endangered her life however, it is also possible that the costs she experienced were outweighed by the benefits she accrued, in terms of establishing or maintaining relationships, or self-enhancement as **Tice et al.** propose.

O'Mara Kunz, Goodnight, and Wilson (O'Mara Kunz et al.) are concerned that the evidence we presented on autoimmune diseases (ADs) is misleading. According to O'Mara Kunz et al., outside of industrialized societies ADs rarely occur and are not more prevalent in females than males. Consequently, they believe that ADs can be better explained by the pregnancy compensation hypothesis than as maladaptive overly strong self-protective immune responses. O'Mara Kunz et al. believe that ADs become more common in industrialized societies because women spend less time gestating and lactating and more time menstruating, thereby changing their sex hormone profiles. This is an intriguing proposition. However, even pre-pubertally more girls than boys develop ADs although the sex bias is less pronounced than in adults (Cattalini, Soliani, Caparello, & Cimaz, 2019). While O'Mara Kunz et al.'s theory therefore can explain the large cross-cultural differences in the prevalence of ADs, the generally accepted understanding of ADs is that they constitute an overreaction of the immune system and worldwide are more common in women. Because threats differ across cultures, ADs may be a reaction to only some types of immunological threats which may be less present in non-industrialized societies.

Another sub-group, including **Fuentes**, **Neuhoff**, **Huntsinger and Raoul**, and **Szocik**, do not believe sufficient evidence exists to provide an evolutionary/biological explanation for the self-protective processes we have identified. Specifically, Fuentes is concerned that we neglect the nuances that occur across demographics and contexts. We acknowledge that the variability is great and do not mean to downplay individual differences. **Troisi** too was concerned that we neglected many individual differences which also contribute to self-protective reactions. Nevertheless, we do not agree with **Fuentes** that SAT is predicated on the nuclear family as a basal human type. Rather, SAT is predicated on the mother–child unit being universal, with female kin and sometimes fathers and sons also participating in childcare (Kramer, 2005; Wood & Eagly, 2002).

Neuhoff believes sex/gender is a continuous variable and that considering it to be binary constitutes poor science and public policy. We acknowledge in our target article that sex/gender is a multidimensional construct and that the studies we found are unfortunately limited by emphasizing binary comparisons. However, we do not believe the complexity of the phenomenon should preclude systematic investigations into biological and evolutionary bases or explanations for sex differences.

Many characteristics associated with sex *typically* covary with chromosomal sex, from the presence of internal and external reproductive structures to sex-typed interests and activities, diseases, gender roles, gender identity, sexual identity, and socialization received. Levels of sex hormones and physical strength however are two characteristics strongly associated with sex chromosomes and not simply by-products as **Neuhoff** asserts. Within-sex variation in levels of sex hormones or physical strength that correlate with degrees of self-protectiveness demonstrates that different components of sex are related to self-protectiveness. It does not negate the value of biological sex in understanding self-protectiveness.

We consider it dangerous for scientific and practical reasons not to acknowledge biological sex differences. Until recently, sex has often not been considered to be an important variable in medical research involving human or nonhuman species. The assumption was that the results from male animals, including men, would apply to female animals, including women. This has led to inferior diagnostic and treatment tools for women, causing untold numbers of girls' and women's deaths (McGregor, 2020). Until girls' and women's lives are examined objectively, and they are considered important in their own right, this will not be remedied.

Nevertheless, our analysis in no way minimizes the importance of understanding sex as a continuous variable. We fully acknowledge that all individuals have some traits that are associated more commonly with the other sex. Therefore, individuals should be understood holistically and not categorized based on any single factor.

Huntsinger and Raoul, similar to **Neuhoff** and **Fuentes**, do not believe sufficient evidence exists to provide an evolutionary/biological explanation for the diverse processes we have identified. Instead, they believe the findings we present are based on stereotypes. While we do not discount the potential role of this and other social and environmental factors, we question whether sex-biased stereotypes exist for the types of evidence we have described. For example, women are less likely to die than men at any age, but more likely to experience some illnesses and chronic conditions. Does this make women less or more healthy than men? Likewise regarding pain, women are typically celebrated for their endurance of pain given how difficult childbirth can be, whereas men in turn are expected to withstand other sorts of pain. What then are sex stereotypes regarding pain? We are not aware of stereotypes regarding sleep, concern about the environment, or fears of disease transmission. Along the same lines, we think it premature to conclude that women categorically "face more chronic strains and stressors" than men, and this is the cause of sex differences in depression or anxiety. By what measures do women suffer more chronic stress than men? If they do however, how can Huntsinger and Raoul then conclude that "the emotional lives of women and men are nearly identical," when evidence points to sex differences in prevalence rates of depression, anxiety, and many other concerns from sexual dysfunctions and paraphilias to eating disorders (Hartung & Lefler, 2019)?

Moreover, there is biological evidence for many of the sex differences we describe. Although females frequently have been excluded from human (McGregor, 2020) and nonhuman (Clayton, 2016) studies, several studies of sex differences with rodents indicate that compared with males, females exhibit stronger immune responses to various pathogens and vaccines (Klein & Flanagan, 2016); exhibit lower pain thresholds (Smith, 2019); and experience more nighttime awakenings (Paul, Dugovic, Turek, & Laposky, 2006; Swift et al., 2020). Likewise, across primate species, females more than males avoid serious social conflicts (Fedigan, 1982; Smuts, 1987).

Nevertheless, we believe that if a behavior is adaptive, then socialization and biology should work together to reinforce it, not counter one another, as **Bleske-Rechek and Deaner** suggest for self-protectiveness. Thus, disentangling the effects of evolved behaviors and environmental inputs constitutes a difficult task that requires as much evidence as possible.

Finally, **Szocik** believes that our analysis could be "used to justify the exploitation and subordination of women in their traditional roles as mothers and caregivers." Obviously, we did not intend that outcome, but it is probably true that any evidence of group differences can be used by one group to disparage another. One response could be to abandon any research on sex differences. We prefer the alternative strategy of understanding the issue, and in this case showing how the evolutionarily significant roles of women as mothers and caregivers illuminate the ultimate and proximate forces that shape women's lives. Harmful gender stereotypes get perpetuated by discounting the role not only of social factors but also of biological ones – leaving us to compare female phenotypes to male reference points rather than considering them as adaptive responses in their own right.

Szocik also believes that we have implied that "that women inherently have lives less worth living than men." This was not our intention, and we strongly disagree with this conclusion. Our paper showed that human females have a series of adaptations that tend to differ from those of men in a consistent pattern. We did not focus on men's lives but had we done so, we would have underscored the difficulties men confront. As examples, boys and men die at every age from disease, accidents, interpersonal conflicts, and other traumatic events more than girls and women do. Men are more likely than women to suffer from addictions, sexual dysfunctions and paraphilias, conduct disorders, attention-deficit hyperactivity disorder, autism, learning disorders (Hartung & Lefler, 2019), and to commit suicide or take such poor care of themselves that they end up dying (Case & Deaton, 2020). Those facts mean we are not surprised by the finding that we cited earlier, that life satisfaction is at least as high among women as among men (Lucas & Gohm, 2000). But whether women or men can be said to have lives less worth living is a judgment that we see as another matter entirely, one that our paper does not address.

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