What can Tradeoffs in Survivorship and Reproductive Effort tell Health Professionals?

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Four general physiological functions compete for resources

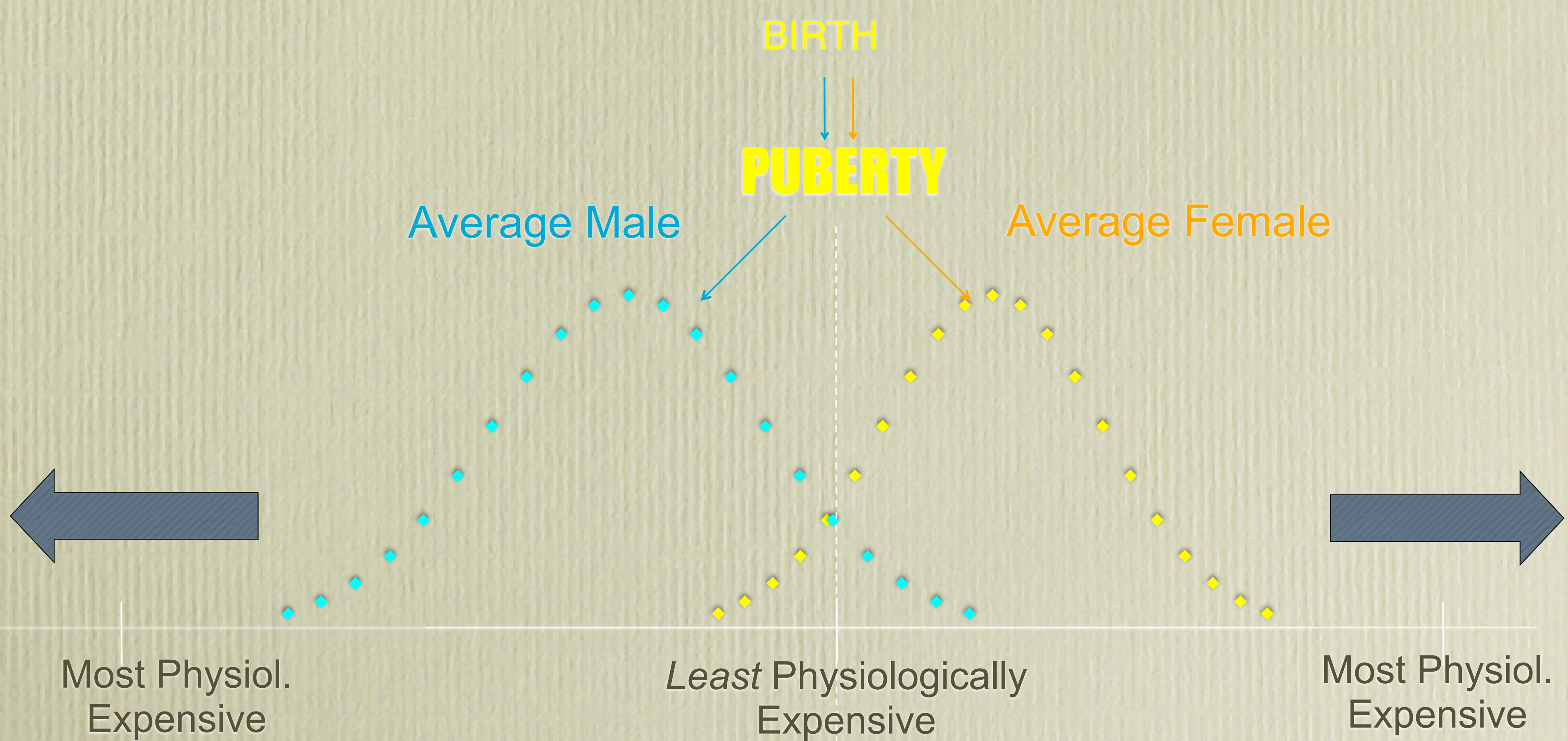
- Growth (i.e., pre-pubertal)
- Maintenance (i.e., immunocompetence)
- Storage (i.e., adipocyte deposition)
- Reproduction (i.e., internal gestation; spermatogenesis; mate attraction & retention)

Survivorship =
Growth; Maintenance; Storage

Reproductive Effort
takes away from somatic effort or survivorship

Catabolic metabolism: breakdown of larger molecules into smaller ones; releases energy.
Anabolic metabolism: building up of tissues such as bone and muscle; requires energy.

Hypothetical Frequency Distributions of Traits Mediated by Anabolic Steroids (sex hormones)



Variation in the Testosterone/ Estrogen hormone ratio

- Testosterone augments anabolically sensitive tissues such as skeletal muscle mass.
- Testosterone suppresses expensive somatic efforts such as immunocompetence.

- Estrogen increases subcutaneous fat.
- Estrogen hyperactivates immunocompetence.

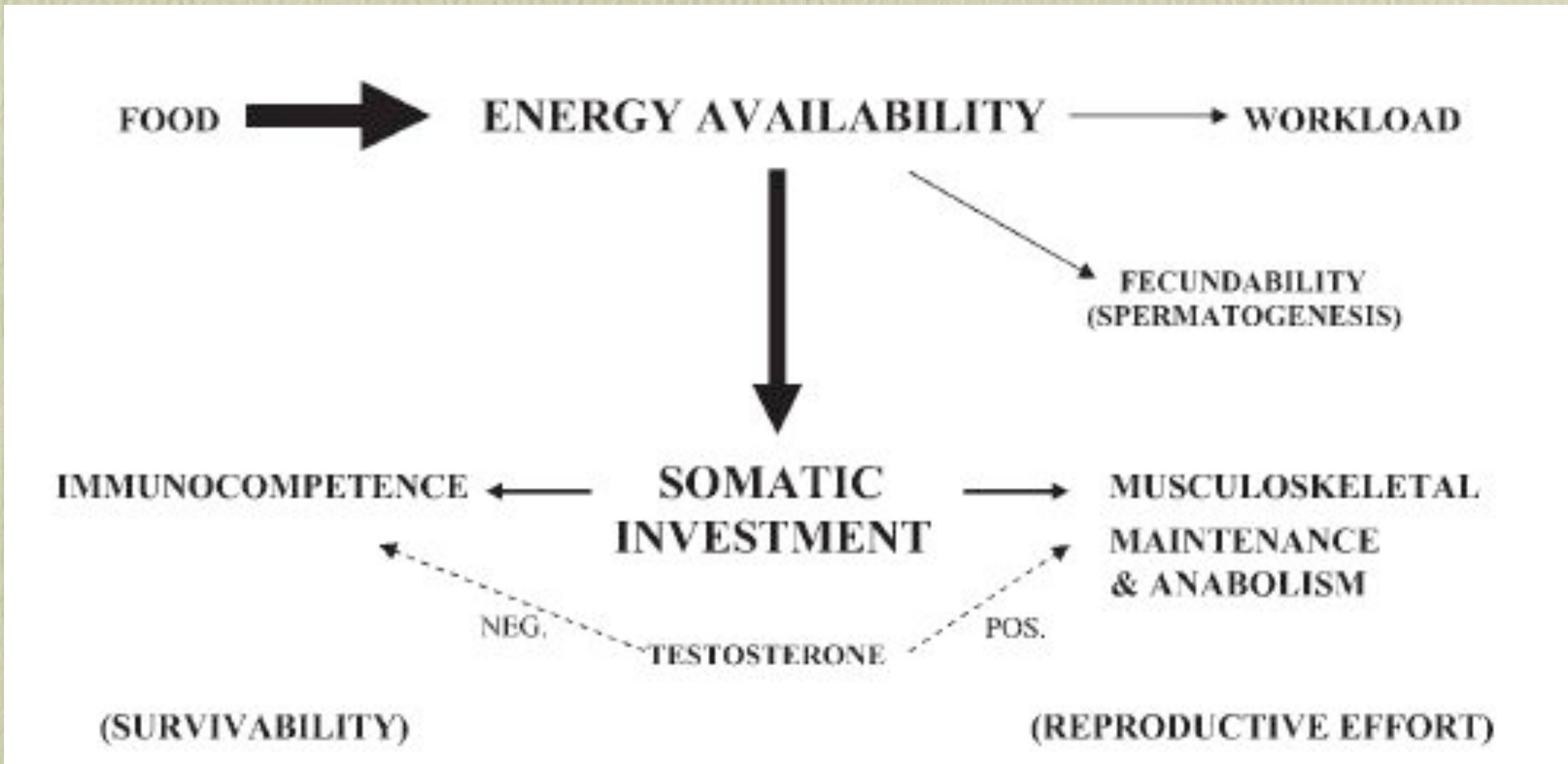
Female somatic condition is strongly linked to her reproductive success, so her expenses (somatic & reproductive) are often in the *same* direction.

- estrogens hyperactivate immunity
- menstruation, internal gestation, childbirth, lactation
- nutritional status predicts egg quality and/or number
- maternal survivorship predicts offspring survivorship

Male reproductive success (across species) results primarily from behavior, often times risky, such that reproductive effort is most often in *opposition* to survivorship.

- male-male competition
- courtship displays, mate attraction
- mate & offspring provisioning & protection

Survivorship vs Reproductive Effort



- Muehlenbein & Bribiescas (2005)

Summary

- Diversion of metabolic energy to support expensive immune function reduces the energy available for reproduction; the cost of reproduction. *The cost for any given organism will depend in part on the likelihood of exposure to a particular pathogen in the environment.*

- In most male mammals, reproductive effort comes in the form of producing and maintaining adequate musculoskeletal function (i.e., muscle mass, red blood cell quantity, cortical bone density, etc.) often to aid in mate attraction and competition with conspecifics for access to mates.

- Maintaining high androgen levels can have fitness costs from causing certain types of immunosuppression that increases morbidity and mortality due to parasitic infection; this is balanced by the reproductive benefits of the androgens.

Endocrine status predicts the activation of anabolically sensitive tissues across many species.

- reviews by Ketterson & Nolan, 1992; Marler & Moore, 1988
- Humans -- Ellison, 2003

Sex Steroids are responsive to available energy and disease risk in the environment.

- ***What happens under energetic stress that results from environmental factors?***

Childhood energetics may affect the testosterone setpoint.

- Testosterone is higher in more industrialized countries (i.e., the U.S. & Europe) as compared to forager, horticultural & pastoral populations in South America (Beall et al., 1992; Bribiescas, 1996), Africa (Bentley et al., 1993; Campbell et al., 1989; Lukas et al., 2004), and Asia (Ellison & Panter-Brick, 1996).

- Higher energetic demands of non-industrialized countries exert developmental effects during adolescence that affect Leydig cell sensitivity to luteinizing hormone (LH) stimulation and testosterone production (Spratt & Crowley, 1988; Bribiescas, 2001).

Energetics of Immune Functions and the 'cost of reproduction'... is testosterone the unifying link?

- ***In 1889*** Calzolari -- male rabbits castrated before sexual maturity had larger thymuses (T cells & cytokines).

- Fact: immunocompetence is expensive -- mitogen stimulation of cellular immunity resulted in a 29% increase in resting metabolic rate in sparrows (the equivalent energy expenditure to produce about half an egg Martin et al. 2003) -- in humans, infection = 10-15% elevation in basal metabolic rate for every degree rise in body temp.

- Fact: Cytokines can directly interact with the Hypothalamic-Pituitary-Testicular axis.

- Fact: Androgen receptors have been identified on T & B cells.

Why are there receptors for androgens on immune cells... ?

- ...to regulate energy allocation.
- Testosterone alters anabolically sensitive tissue including skeletal muscle mass & greater fat catabolism, while suppressing certain immune responses.

In Vitro Effects of Testosterone on Immune Cells

TABLE 4. In vitro experiments of testosterone and immune function

Effects of testosterone	References
1. Alter T-lymphocyte function	Mendenhall et al. (1990); Olsen and Kovacs (1994); Benten et al. (1999); Samy et al. (2000); Maurer et al. (2001)
2. Alter the $CD4^+$ $CD8^+$ T-cell ratio in favor of $CD8^+$ cells	Olsen et al. (1991); Weinstein and Bercovich (1981)
3. Increase $Lyt2^+$ suppressor T-cell populations	Weinstein and Berkovich (1981)
4. Reduce T-helper cell function	Grossman et al. (1991); Wunderlich et al. (2002)
5. Alter T-cell function by inducing a rapid influx in intracellular free Ca^{2+} concentration in activated T cells	Benten et al. (1997); Wunderlich et al. (2002)
6. Reduce B-cell lymphopoiesis and affect antibody production	Olsen and Kovacs (1996)
7. Preferentially alter the development of a $CD4^+$ type-1 phenotype of peripheral lymphocytes and cytokines	Daynes et al. (1991); Huber et al. (1999); Giltay et al. (2000)
8. Inhibit the expression of nitric oxide synthase in murine macrophages	Friedl et al. (2000)
9. Impair phagocytic capacity of macrophages and inhibit nitrite release by macrophages	Chao et al. (1994); Chao et al. (1995); Straub and Cutolo (2001)
10. Diminish pro-inflammatory cytokine production by macrophages	Daynes and Araneo (1991); Grossman et al. (1995); Lin et al. (1996); Smithson et al. (1998); Straub and Cutolo (2001); Burger and Dayer (2002)

- Muehlenbein & Bribiescas (2005)

Return to the statement:
Sex steroids are responsive to available energy and disease risk in the environment.

- What happens under energetic stress that results from environmental factors?
- ***What is happening under infection?***

Compare Male to Female Immunocompetence

- "Male-biased" refers to the prevalence & intensity of infection.

TABLE 1. Studies evaluating immunocompetence in males versus females

Host species/parasite species	Study design	Outcomes	References
1. Numerous vertebrate hosts/ helminth infections	Meta-analysis	Male-biased	Poulin (1996)
2. Numerous hosts/parasites	Meta-analysis	Male-biased in 8 of 10 orders	Moore and Wilson (2002)
3. Human/filarial infections	Meta-analysis	Male-biased in 43 of 53 studies	Brabin (1990)
4. Reindeer (*Rangifer t. tarandus*)/ warble flies (*Hypoderma tarandi*)	Comparing larval abundance	Male-biased	Folstad et al. (1989)
5. Various lizard hosts/malaria (*Plasmodium*)	Infection prevalence	Male-biased	Ayala and Spain (1976); Schall and Vogt (1993); Schall (1996)
6. Hamster/*Leishmania* sp.	Comparing parasite burden	Male-biased	Travi et al. (2002)
7. Japanese macaques (*Macaca fuscata*)/ various infectious diseases	Comparing likelihood of mortality	Male-biased	Fedigan and Zohar (1997)
8. House cricket (*Acheta domesticus*)/ *Serratia liquefaciens*	Comparing susceptibility to infection	Male-biased	Gray (1998)
9. Scorpionflies (*Harpobittacus* sp.)/ various infections	Comparing susceptibility to infection	Male-biased	Kurtz et al. (2000)
10. Indian soft-furred rats (*Millardia meltada*)/ nematode infections	Macrophage activity	Less effective in males	Tiuria et al. (1995)
11. Humans and various other species	Immunoglobulin levels	Lower in males	Lichtman et al. (1967); Kacprzak-Bergman (1994); Olsen and Kovacs (1996)
12. Mice	Splenocyte blastogenic response to T-cell mitogens	Lower in males	Krzych et al. (1981)
13. Various species	Antibody responses to infection	Lower in males	Schuurs and Verheul (1990)
14. Various species	Cytokine responses	Lower in males	Bijlsma et al. (1999)
15. Numerous avian hosts/parasites	Meta-analysis	No sex differences in prevalence	McCurdy et al. (1998)
16. Mouse/*Taenia crassiceps*	Comparing susceptibility	Female-biased	Gomez et al. (2000)
17. Meadow voles (*Microtus pennsylvanicus*)	IgM responses to keyhole limpet hemocyanin	Greater response in males	Klein and Nelson (1998)
18. Great tits (*Parus major*)/*Haematozoa*	Prevalence rates	Higher in females	Norris et al. (1994)
19. Humans/various autoimmune diseases	Incidence rates	Higher in females	Da Silva (1995)

- Muehlenbein & Bribiescas (2005)

Does it matter which component of the immune system is measured and type of pathogen?

- Innate immunity - eliminates foreign particles from invasion of the host (mucous, skin, resident flora, humoral factors such as lysozymes and the complement system {inflammatory response, lysis), and phagocytes, natural killer cells & eosinophils. Macrophages are a major part of innate immunity; phagocytize, cytokine secretion, chemotaxis, and antigen processing & presentation.

- Adaptive immunity - development of secondary responses for subsequent exposures; lymphocytes (B & T cells); B = humoral immunity (memory cells involved in immunoglobulin / antibody production - IgG bacteria, IgM inflammatory response & lysis of complement system, IgA mucosal surfaces, IgE helminthes); T cells = cellular immunity (cytotoxic T/CD8+ destroy infected host cells; helper T/CD4+ secrete cytokines: Th-1 cytokines activate cellular immunity via T cells & Th-2 cytokines induce humoral immunity via B cells, Th-1 & Th-2 antagonistic but may act synergistically, i.e., gut inflammation with helminthes.

Non-human Castration vs Testosterone Supplementation...

TABLE 3. Studies evaluating associations between immunocompetence and castration or testosterone supplementation

Host species (sex)	Treatment	Parasite species	Outcome	Reference
1. Rabbit	Castration	NA	Increased thymus size	Calzolari (1889)
2. Mouse	Castration	NA	Increased thymus size	Olsen et al. (1991)
3. Mouse	Castration followed by mitogen	NA	Increased antibody production and splenocyte proliferation	Schuurs and Verheul (1990)
4. Mouse	Castration followed by burn	NA	Increased cellular immunity	Messingham et al. (2001)
5. Mouse	Castration followed by trauma	NA	Increased cellular immunity	Remmers et al. (1997); Angele et al. (1998); Wichmann et al. (1997)
6. Mouse	Castration	NA	Depressed suppressor T-cell function	Weinstein and Berkovich (1981)
7. Deer mouse	Castration	NA	No effect on lymphocyte proliferation	Demas and Nelson (1998)
8. Western fence lizard	Castration	*Plasmodium mexicanum*	No effect on infection level	Eisen and DeNardo (2000)
9. Siberian hamster	Castration followed by phytohemagglutinin	NA	Decreased lymphocyte proliferation	Bilbo and Nelson (2001)
10. Mouse (m)	Testosterone	*Plasmodium chabaudi*	Decreased proportion of $CD4^+$ cells and immunoglobulins	Benten et al. (1993)
11. Mouse (f)	Testosterone followed by zymosan and phorbol–myristate–acetate	*Plasmodium chabaudi*	Reduced capacity of peritoneal cells to generate reactive oxygen intermediates	Benten et al. (1997)
12. Soft-furred rat (f)	Testosterone	*Nipostrongylus brasilnesis*	Reduced worm expulsion	Hadid et al. (1995); Tiuria et al. (1995)
13. Mouse (m)	Testosterone	Tapeworm sp.	Increased tapeworm egg production	Folstad and Karter (1992)
14. Mouse (f)	Testosterone	*Strongyloides ratti*	Increased susceptibility	Watanabe et al. (1999)
15. Bank vole	Testosterone	*Ixodes ricinus*	Reduced acquired immune response	Hughes and Randolph (2001)
16. Wood mouse	Testosterone	*Ixodes ricinus*	Reduced acquired immune response	Hughes and Randolph (2001)
17. Sprague-Dawley rat (m)	Testosterone followed by phytohemagglutinin	NA	Suppressed skin-test response	Mendenhall et al. (1990)
18. Sand lizard (m)	Testosterone	*Ixodes* sp.	Increased tick load	Olsson et al. (2000)
19. Northern fence lizard (m)	Testosterone	Ectoparasites	Increased ectoparasite loads	Klukowski and Nelson (2001)

(Continued)

...Non-human Castration vs Testosterone Supplementation, cont'd.

- In sum, testosterone was significantly associated with ectoparasites but not endoparasites.

TABLE 3. Continued

Host species (sex)	Treatment	Parasite species	Outcome	Reference
20. *Psammodromus* lizard	Testosterone	*Ixodes* sp	Increased tick loads	Salvador et al. (1996)
21. Moorhen (m/f)	Testosterone	*Menopon gallinae*	Higher infestation intensity	Eens et al. (2000)
22. Greenfinch (m)	Testosterone	Sindbis virus	No effect on viremia or antibody response	Lindstrom et al. (2001)
23. European Starling (f)	Testosterone followed by tail feather plucking	NA	Suppressed tail feather regrowth	De Ridder et al. (2002)
24. European Starling (m/f)	Testosterone followed by keyhole limpet hemocyanin	NA	Suppressed antibody response	Duffy et al. (2000)
25. European Starling (m)	Testosterone followed by phytohemagglutinin	NA	Suppressed cell-mediated response	Duffy et al. (2000)
26. European Starling (f)	Testosterone	*Staphylococcus aureaus*	Higher infections	De Ridder et al. (2002)
27. Superb fairy-wren (m)	Testosterone followed by sheep red blood cells	NA	Decreased likelihood of antibody response	Peters (2000)
28. Black-headed gull	Testosterone followed by sheep red blood cells	NA	No effect on antibody response	Ros et al. (1997)
29. Veal calves	Testosterone followed by human serum albumin	NA	No effect on antibody response	Gropp et al. (1976)
30. Dark-eyed junco (m)	Testosterone	NA	Suppressed antibody- and cell-mediated immunity	Casto et al. (2001)
31. Broiler chicken	Testosterone	NA	Inhibition of macrophage phagocytosis and lymphocyte proliferation	al-Afaleq and Homeida (1998)
32. Red jungle fowl	Testosterone	NA	Decline in lymphocyte counts	Zuk et al. (1995)
33. Barn swallow	Testosterone	NA	Decline in immunoglobulin levels but no effect on total absolute leukocyte counts	Saino et al. (1995)
34. Human (m)	Testosterone	NA	No effect on C-reactive protein levels	Singh et al. (2002)
35. Human (m)	Testosterone	HIV	No effect on $CD4^+$ and $CD8^+$ cell counts or HIV RNA copy number	Bhasin et al. (2000)

- Muehlenbein & Bribiescas (2005)

Fact: androgens interact with the immune system differentially with regard to gender.

New Directions for Medical Research:

- In males, there will be strong sexual selection to control those parasites that are detectable by females (innate components of immunity?).
- In females, there will be strong natural selection to control her immune response such that her capacity to carry out internal gestation & the following energetic demands of lactation is maximized.

Blood circulating level of testosterone is not always a good method to find immune effects…

TABLE 2. Studies evaluating associations between immunocompetence and endogenous testosterone levels in males

Host species/parasite species or treatment	Outcomes	References
1. Mouse/*Babesia microti*	Negative correlation between testosterone and resistance	Barnard et al. (1994)
2. Mouse/*Brugia malayi*	No correlation between testosterone and worm burden	Ganley and Rajan (2001)
3. Vole (*Microtus* sp.)/*Trichinella spiralis*	Testosterone levels did not differ between parasitized and unparasitized animals	Klein et al. (1999)
4. Vole (*Microtus* sp.)	Testosterone levels unrelated to splenocyte proliferation	Klein et al. (1997)
5. Barn swallow (*Hirundo rustica*)/ intestinal parasites	Negative correlation between testosterone and parasite load	Saino and Moller (1994)
6. Barn swallow (*Hirundo rustica*)/ ectoparasites	No association between testosterone and prevalence and intensity of infections	Saino and Moller (1994); Saino et al. (1995)
7. Barn swallow (*Hirundo rustica*)	No association between testosterone and antibody production	Hasselquist et al. (1999)
8. European starling (*Sturnus vulgaris*)/ keyhole limpet haemocyanin	Negative correlation between testosterone and antibody response	Duffy and Ball (2002)
9. Red-winged blackbird (*Agelaius phoeniceus*)/ectoparasites and endoparasites	No association between testosterone and parasite load	Weatherhead et al. (1993)
10. Human	No association between testosterone and T or B lymphocytes; positive correlation between testosterone and $CD4^+$ cell numbers; negative correlation between testosterone and IgA levels	Granger et al. (2000)
11. Human/HIV	Negative correlation between testosterone and TNFα production	Roubenoff et al. (2002)
12. Rhesus macaques (*Macaca mulatta*)	Testosterone levels highest in Fall, and IFNγ lowest in Winter	Mann et al. (2000)
13. Long-tailed macaques (*Macaca fasicularis*)/ Venezuelan Equine Encephalitis virus	Pre-exposure testosterone levels positively correlated with post-exposure viremia	Muehlenbein (2004)
14. Common chimpanzee (*Pan troglodytes schweinfurthii*)/intestinal parasites	Positive association between testosterone and intestinal parasite richness	Muehlenbein (2004)
15. Human/chest pain and spleen complaints	Testosterone predicted presence of complaints	Campbell et al. (2001)
16. Human/*Plasmodium falciparum*	Testosterone predicted resistance to parasitemia	Kurtis et al. (2001)
17. Human/*Plasmodium vivax*	Positive association between testosterone and parasitemia	Muehlenbein et al. (2005)

- Muehlenbein & Bribiescas (2005)

High testoterone is not always associated with general immunosupression.

- Some males (in good condition or having 'good genes') may be healthy enough to be able to withstand high testosterone and still keep parasite loads to a minimum.
- Datasets may be bimodal -- yielding statistically insignificant results when condition/health is not assessed.
- Singh et al.(2002): administered varying doses of testosterone over 20 weeks to 61 healthy men and looked at cardiovascular risk, finding no effect on insulin sensitivity, plasma lipids, apolipoproteins, or C-reactive proteins.

Selected studies in humans that found effects of testosterone on immune function.

- Granger et al. (2000): testosterone and IgA levels negatively correlated in healthy military men (N = 4415).

- Campbell et al. (2001): testosterone levels in pastoralists in NW Kenya predicted chest pain (tuberculosis) and spleen complaints (malaria) in industrialized Turkana but not nomadic Turkana (where energy demands presumedly are high).

- Kurtis et al. (2001): testosterone predicted resistance to *P. falciparum* in male Kenyans.

- Muehlenbein at al. (2005): Hondurans infected with *P. vivax* had lower testosterone than age-matched non-infected Hondurans.

- Singh et al. (2000): Testosterone-treatment in HIV-infected men experiencing wasting showed increased voluntary muscle strength, lean body mass, and thigh muscle volume.

Perhaps not a direct tradeoff so much as an "Immunodistribution"

- Redistribution or a temporary shifting of immune cells to compartments where they are likely to be "more useful, such as the skin or body openings" [*perhaps more supportive of reproductive success and the specific demands of a particular mating system and/or particular pathogen expression; innate vs adaptive response*].

- Braude et al. (1999): Leukocytes are temporarily shunted to different compartments of the immune system in response to testosterone.

What about Female Immunocompetence?

- Fact: females across most species (reptiles, birds, mammals) are not as susceptible to infection, in both prevalence and intensity.
- Females of various species often exhibit higher adaptive immune components: higher serum immunoglobulins, higher splenocyte blastogenic response to T cell mitogens, and in general, are better able to mount an antibody response than males.
- As well, females exhibit higher CD4+ helper T cel Th-2 cytokine responses.
- Females suffer from greater incidence of autoimmune diseases (i.e., rheumatoid arthritis; Grave disease, lupus, Addison's disease) in today's modern hygienic environment.

Take Home Message

- Sex steroids alter immunocompetence.
- Immune components alter reproductive effort.
- High energy demands may divert energy from the immune response and reallocate to reproductive effort, and vice versa depending on infection load and environment.
- Future directions: knowing pathogen behavior & health condition may help characterize the nature of SE/RE tradeoffs.

Can knowing about survivorship and reproductive tradeoffs help medicine? How?

- Theory-driven approach to disease is powerful for etiology.
- Physician diagnosis may be quicker and more accurate if the evolutionary design for fundamental physiological tradeoffs is considered.
- Consideration of gender, age, and immune status may illuminate common physiological paths to breakdown.

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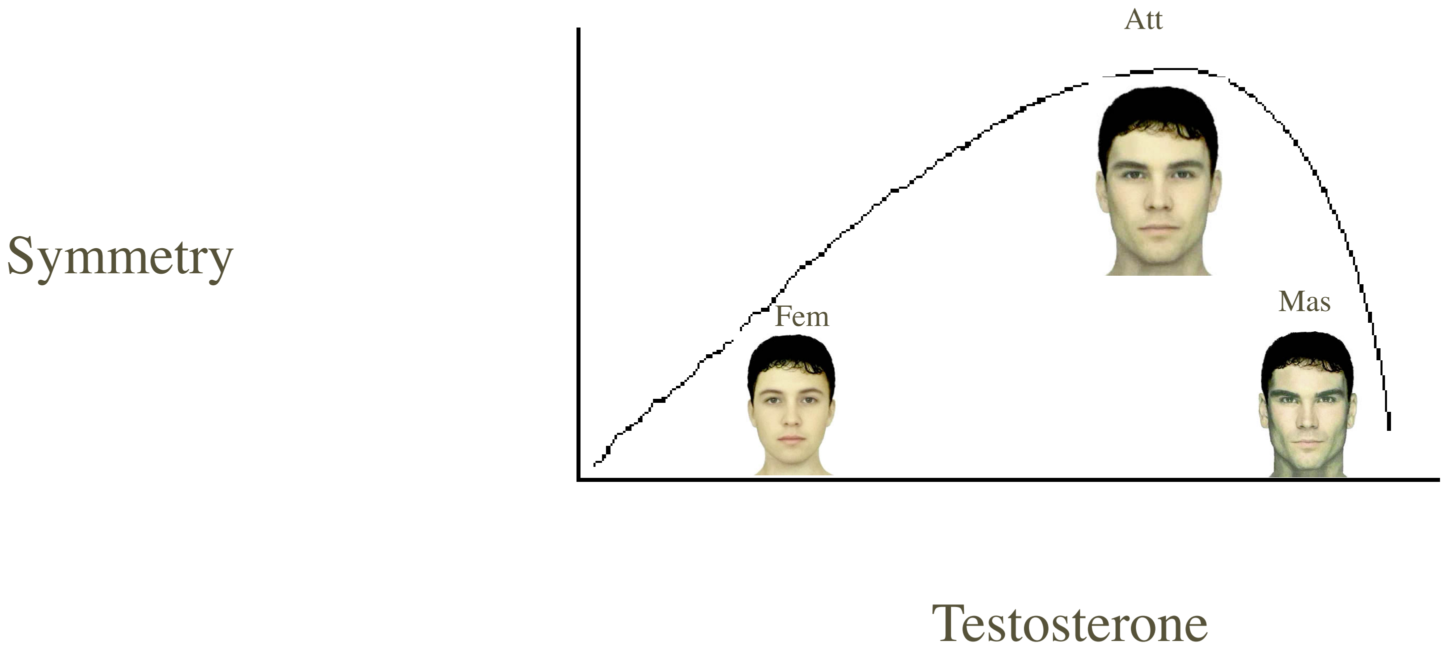
Singh et al. (2000): Testosterone-treatment in HIV-infected men experiencing wasting showed increased voluntary muscle strength, lean body mass, and thigh muscle volume.

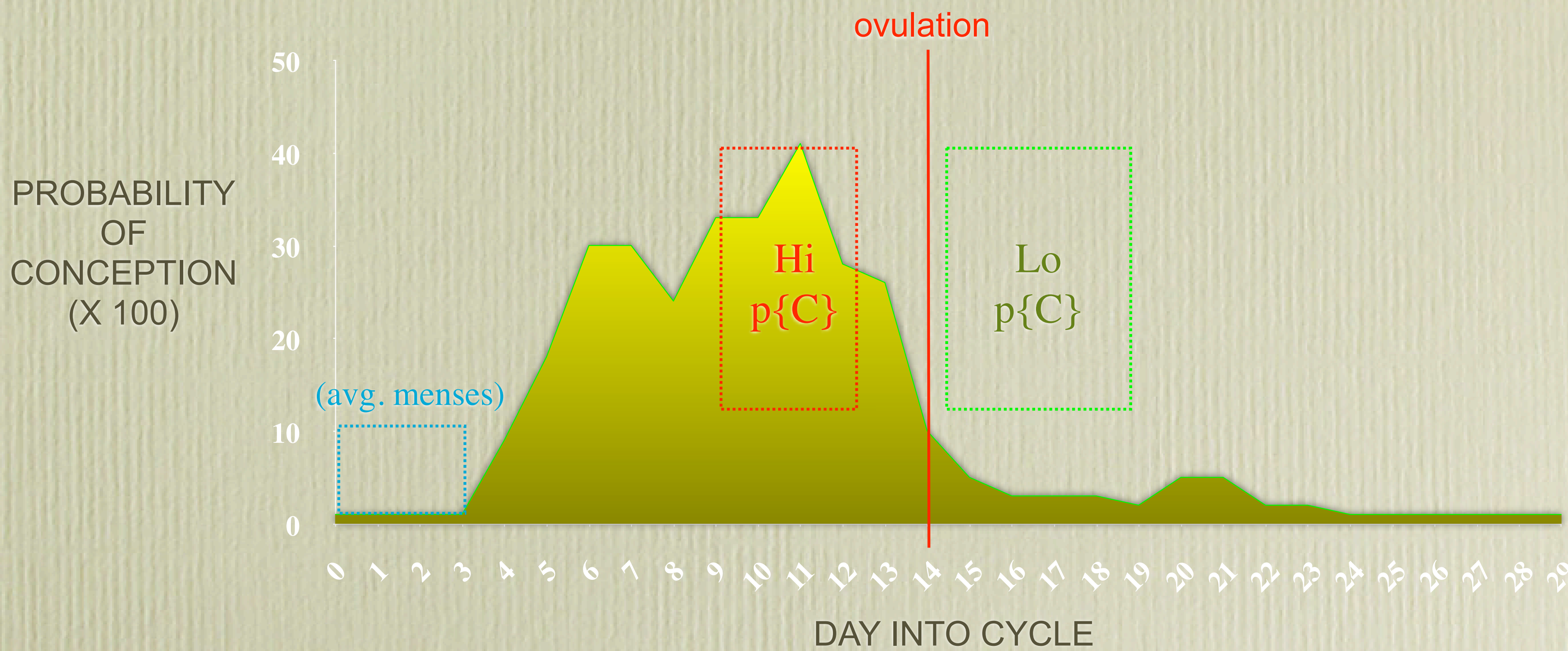
Predictions with regard to health condition

- Those males with the highest testosterone should have more parasites (i.e., they are trading off reproductive performance against immunity from parasites)
- OR, those same males may have fewer parasites (i.e., only resistant males could afford to elevate their testosterone.
- If both are going on in any given population of study, then either no results or mixed results may be obtained if condition is not considered (i.e., Fluctuating Assymetry).

Hypothetical Male Population
(expected Testosterone by Symmetry interaction)



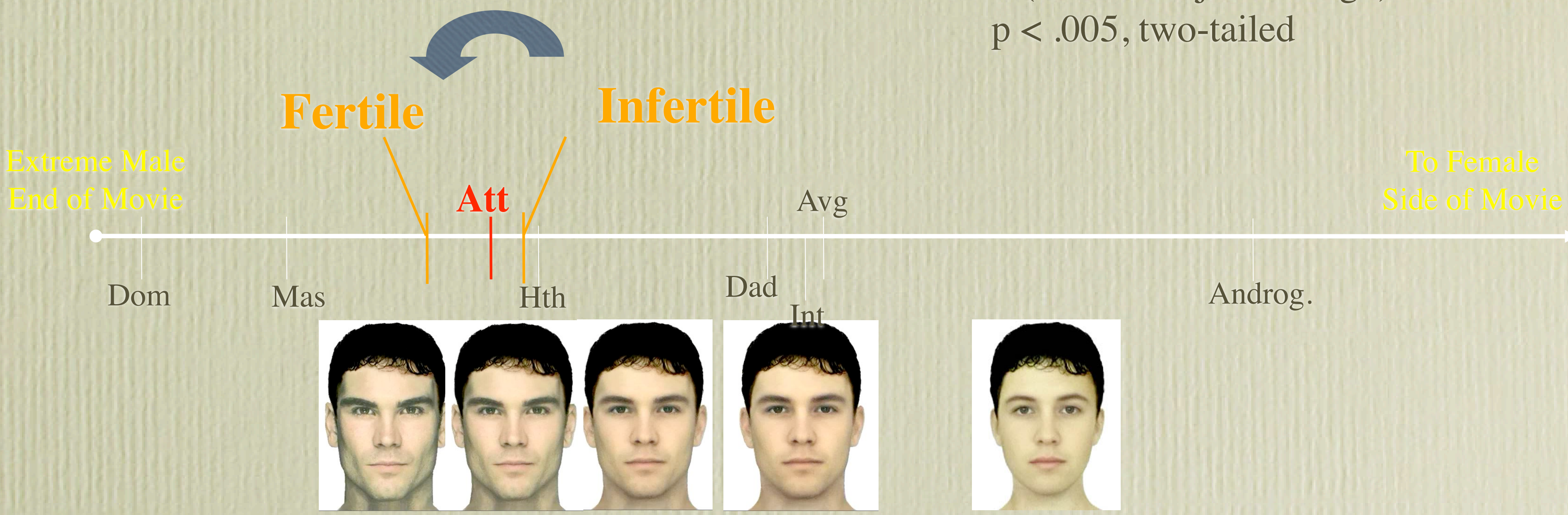
Women's actuarial probability of conception as a function of day in ovulatory cycle



*From Jochle (1973). Total *N* > 1800

Within Females, a Shift in Attractiveness with Change in Risk of Conception

N = 34 (within subjects design)
$p < .005$, two-tailed



Dom ≠ Mas ≠ Att/Hth ≠ Dad/Int/Avg ≠ Androgynous

Relevant Results

1. The attractive male face was the same as the healthy male face, suggesting perceived genetic quality may be highly linked to perceived attractiveness.

2. Only the attractive male face (not other faces) shifted significantly toward higher masculinity with conception risk, suggesting that some traits associated with masculinity are separate from genetic quality.

Theoretical Mating Domains

Mate Choice

GENETIC QUALITY	SPECIFIC ABILITIES
• indirect benefits re: viability of offspring • supports developmental stability and/ or immuno-competence	• direct benefits to chooser or offspring (e.g., food, parental care, status, or protection, intelligence).

In process of being analyzed: characteristics of the female perceivers

- Intra-uterine exposure to androgens (2D:4D)
- BEM score (Masc/Fem)
- Pubertal exposure to sex hormones (facial photos)
- Self-rated Attractiveness
- Sociosexual Orientation
- Post-study menses (allowing analysis of irregular cycling women)

Life History Variables

- Age of menarche
- Age of first coitus
- Presence of each parent throughout childhood
- Reported childhood physical or sexual abuse
- SES, parent education
- Self-projected mortality
- Current nearby kin

Digression: Evolutionary Questions relevant to both Physical & Mental Health

- Given human sociality and historically critical codependence on conspecifics for survival and reproduction, the number of non-kin and kin in proximity of an individual may help in diagnoses.

- For example, mild depression can be an honest signal to positive fitness correlates (social parters; relatives) for support in maximizing our personal niche and (subconscious) capacity for reproductive success. {I.e, post-partum drops in thyroid hormone induce depressive systems}

- If a lack of positive fitness correlates exist in proximity, does the physiology change to intensify or postpone reproductive efforts? {I.e., tiny benign pituitary tumors that secrete prolactin (the 'bonding hormone') are found in 20% of autopsies incidental to death! what is going on?}

Why do females value masculinity less at low risk of conception?

- Hormone markers are expected to function in concert with other cues of good genes (e.g., symmetry), but, hormone markers appear to carry additional cues that are likely to be specific to forces of sexual selection.

Females were asked to rate their chosen faces (varying in masculinity) on behavioral traits:

Threatening   Physically Attractive

Cooperative   Volatile   Sexually Exciting   Helpful Controlling Healthy

Trustworthy   Manipulating   Protective   Selfish Coercive Dominant   Impulsive

Sensitive   Wealthy Intelligent

Results of Rotated Components

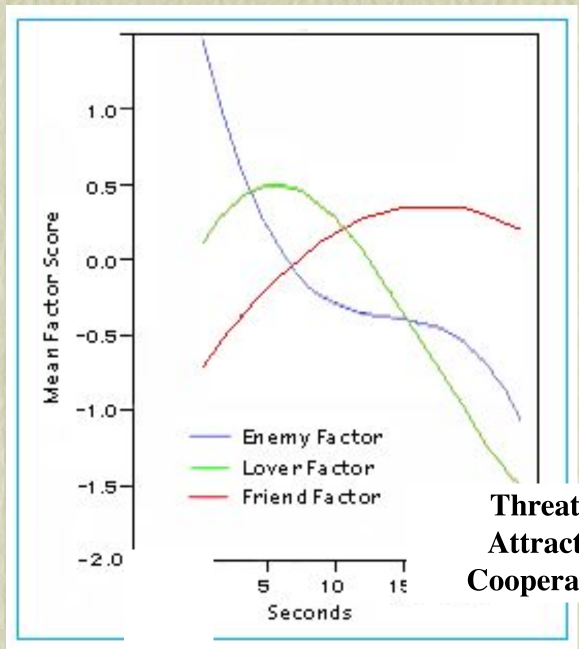
(including $r > .60$)

Factor One	*Factor Two*	*Factor Three*
Threatening (.90)	**Ph.Attractive (.91)**	**Cooperative (.84)**
Volatile (.87)	**Sex. Exciting (.88)**	**Helpful (.84)**
Controlling (.85)	**Healthy (.68)**	**Trustworthy (.80)**
Manipulating (.84)	**Protective (.63)**	**Sensitive (.78)**
Coercive (.81)		
Dominant (.79)		
Selfish (.78)		

Principal Components Analysis of Personality Ratings

Three factors account for 75% of the variance.

- Threat (factor 1)
- Attract (factor 2)
- Cooperate (factor 3)



Threat Factor
Attract Factor
Cooperate Factor

Testosterone

The question is, what problems in human ancestral environments might testosteronization solve?

- The threat vs cooperate components associated with masculinity suggest that selective forces in ancestral environments were at times in opposition.
- E.g., Good social partners are expected to be willing to invest as well as protect, but if the genetic support for ability to do so is not there, tradeoffs in one or the other direction are expected. Females are expected to be sensitive to these tradeoffs.

Methodology

- Forced Choice Paradigm - eight faces, with nine variants each, were ranked in attractiveness by placing each of the nine variants on boxes that represented low attractiveness (1) to high attractiveness (9).

- Within Subjects Design - the same females returned at varying points in their menstrual cycles while completing credit for introductory psychology at UNM.

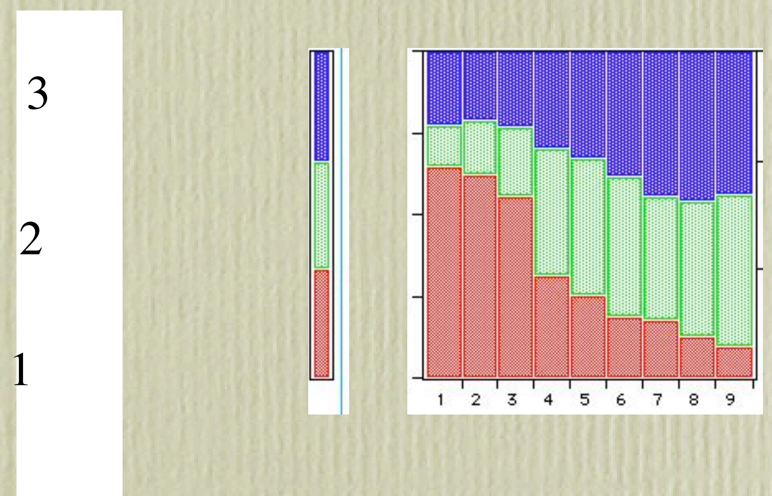
Expected Patterns

Masculinity may reflect additional traits above and beyond genetic quality, and these additional traits may be driven by female condition (past and present circumstances) resulting in a non-linear function.

- Symmetry may be more strongly effected by conception risk than masculinity.
- More variance is expected for attractiveness rankings of masculinity than for symmetry.

Not surprisingly, assymmetrical faces ranked lower in attractiveness than symmetrical faces.

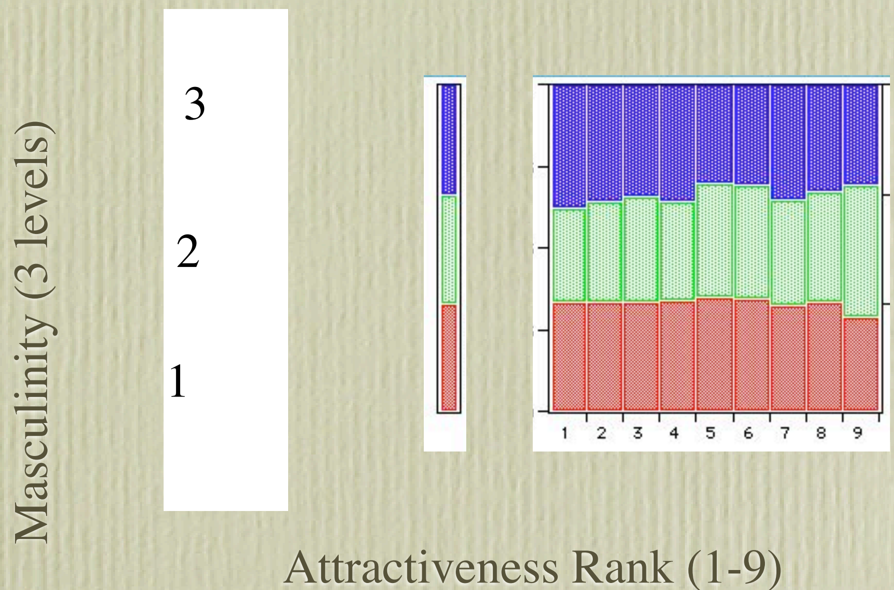
Symmetry (3 highest)



Attractiveness Rank
(9 highest)

- Symmetry, 3 levels
- Attractiveness, 9 levels

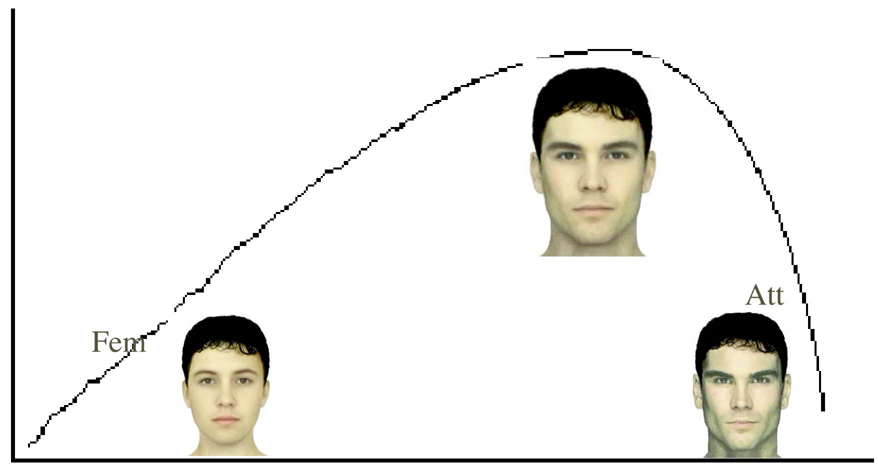
Preliminary Analysis of Masculinity By Attractiveness Rank



- Masculinization appears to have little effect on attractiveness.

Hypothetical Male Population
(expected Testosterone by Symmetry interaction)

Symmetry



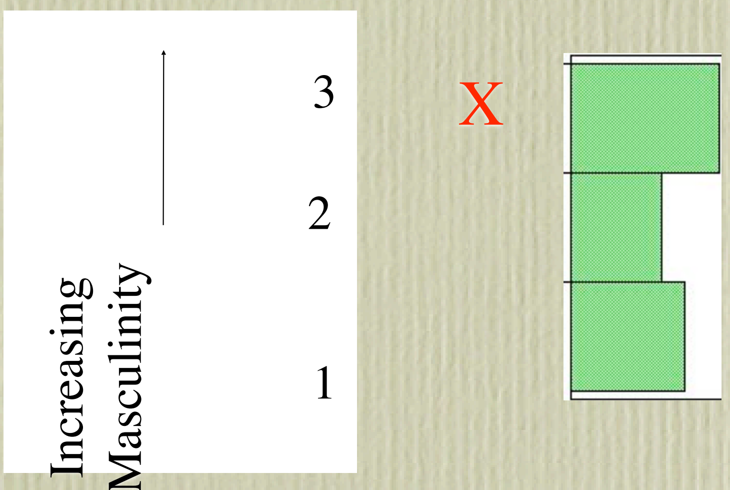
Mas

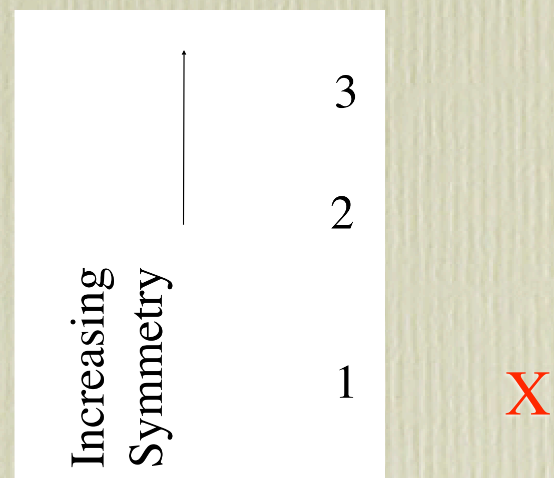
Testosterone

If cues of genetic quality are absent, but potential threat cues are present, faces may be perceived with caution.

- After ranking all nine versions of a particular male, females were asked to chose from the nine versions one last face: "the face that appears most likely to be a criminal, where criminality could mean major offenses like murder or rape or simply someone who is dishonest or cheats".

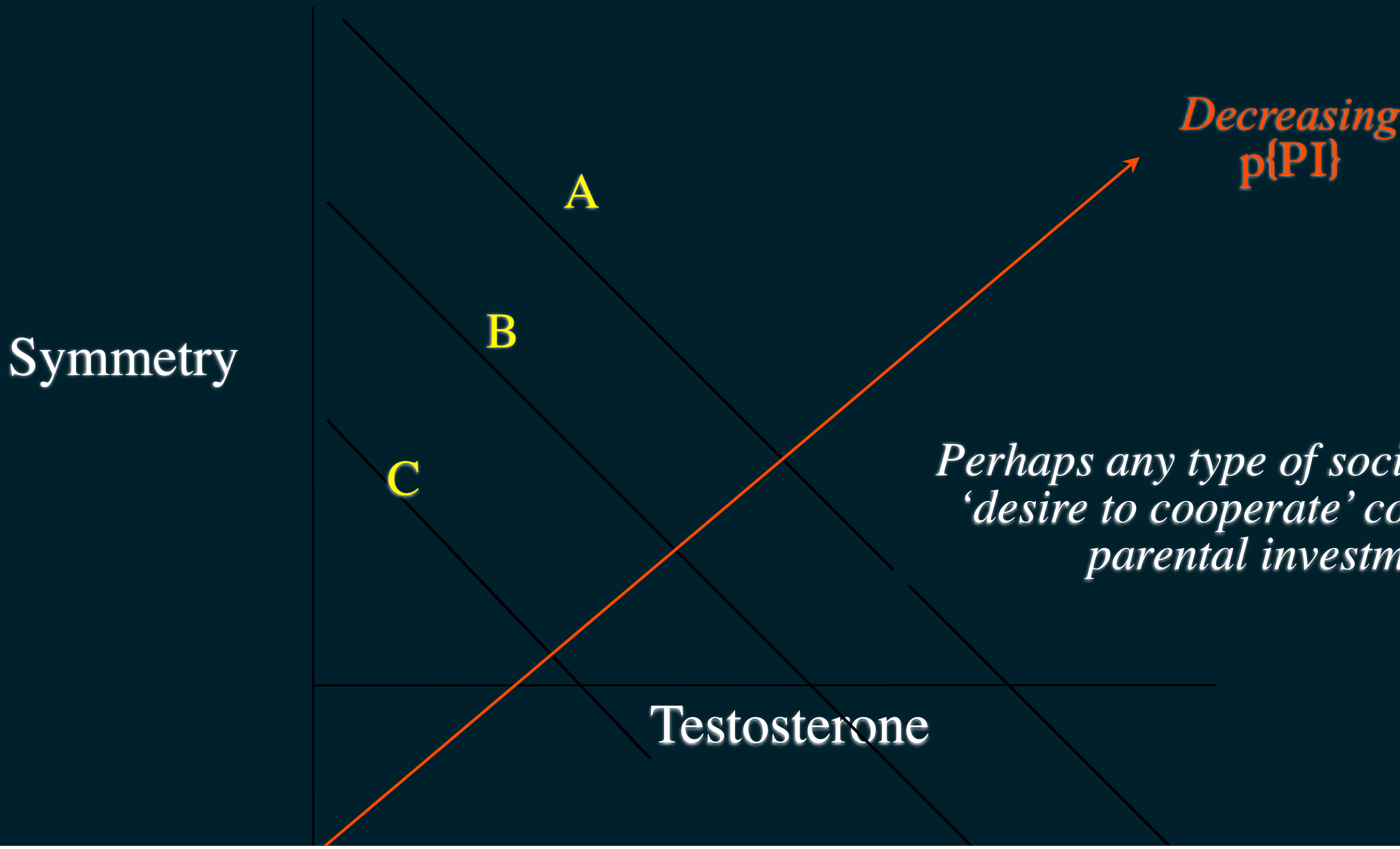
Perceived Criminality Effect on Masculinity and Symmetry





Out of the 72 subtle variants of masculinity and symmetry,
females tended to choose more masculine and less symmetrical faces in answer to the criminality question (not significant).

Working Model



Perhaps any type of social willingness or 'desire to cooperate' could stand in for parental investment here.