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RESEARCH ARTICLE

Can Persistence Hunting Signal Male Quality? A Test Considering Digit Ratio in Endurance Athletes

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Abstract

Various theories have been posed to explain the fitness payoffs of hunting success among hunter-gatherers. 'Having' theories refer to the acquisition of resources, and include the direct provisioning hypothesis. In contrast, 'getting' theories concern the signalling of male resourcefulness and other desirable traits, such as athleticism and intelligence, via hunting prowess. We investigated the association between androgenisation and endurance running ability as a potential signalling mechanism, whereby running prowess, vital for persistence hunting, might be used as a reliable signal of male reproductive fitness by females. Digit ratio (2D:4D) was used as a proxy for prenatal androgenisation in 439 males and 103 females, while a half marathon race (21km), representing a distance/duration comparable with that of persistence hunting, was used to assess running ability. Digit ratio was significantly and positively correlated with half-marathon time in males (right hand: $r = 0.45$, $p<0.001$; left hand: $r = 0.42$, $p<0.001$) and females (right hand: $r = 0.26$, $p<0.01$; left hand: $r = 0.23$, $p = 0.02$). Sex-interaction analysis showed that this correlation was significantly stronger in males than females, suggesting that androgenisation may have experienced stronger selective pressure from endurance running in males. As digit ratio has previously been shown to predict reproductive success, our results are consistent with the hypothesis that endurance running ability may signal reproductive potential in males, through its association with prenatal androgen exposure. However, further work is required to establish whether and how females respond to this signalling for fitness.

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Introduction

Hunting and reproductive success

The high value placed by females on male ability to acquire resources has been well documented [1]. This is evident in pre-industrial human societies, where males exhibit a positive relationship between status and number of surviving offspring. Such observations have been made across the continents of Africa, South America and Asia [2–4]. It has been suggested that

the same is true of contemporary Western society; increasing income has been shown to have a significant effect on male reproductive success and desirability as a marriage partner [1,5–7].

Prior to agriculture, hunting may have represented an important means by which male resourcefulness could be demonstrated. Food is inexorably linked to status in many cultures around the world [8], and there is evidence that superior hunters enjoy social prestige within the community [9]. Indeed, successful hunters have been shown to enjoy higher reproductive success [10,11]. Hunting may therefore be motivated by male-male competition [12]. Smith [4] has reviewed quantitative links between hunting ability and fitness-related factors such as fertility, offspring survivorship and number of mates, and qualitative links between hunting success and knowledge of hunting ability within communities. However, it is not clear whether it is the high social status of hunters (which reflects their ability to acquire resources), or the actual resources they obtain, that provides the mechanism linking hunting success with reproductive fitness.

Theories posed to explain the fitness payoffs of hunting success include the "direct provisioning" hypothesis, which asserts that successful hunters are more able to share food with their mate and children, thereby enhancing fertility and offspring survivorship through physiological mechanisms. In accordance with this theory, the offspring of successful hunters may indeed be better nourished [13]. Recent endocrine data from subsistence populations has revealed that while testosterone levels increase upon a successful kill, this increase is not associated with the number and size of kills or the presence of an audience beyond the hunter's family [14]. These findings are consistent with the direct provisioning model; meat provisioning enhances reproductive success either directly [11], or indirectly through political alliances and other benefits stemming from the community's desire to retain a successful hunter as a neighbour [15–18]. Although this theory has intrinsic appeal, the egalitarian organisation of many forager societies ensures that this nepotistic distribution of food is not consistently observed [3]. While some male hunters are more effective than others, meat is widely distributed throughout the group. As a result most of the food consumed is caught by a man outside one's own nuclear family, such that the hunter's own family may receive no more meat than anyone else [3]. Such sharing has been attributed to a means of maintaining social identity, and has been considered a defining characteristic of hunter-gatherer behaviour [19]. Food sharing also serves as a mechanism to deal with fluctuations in food availability [20]. A hunter may exchange a short-term food surplus for receipt of food in the future should his own hunting efforts fail; a phenomenon known as the reciprocal altruism [21]. When food resources are scarce and hunting success unpredictable, food sharing is prevalent as a type of culinary insurance policy, as seen in the Inuit of Akalivik [22]. However, food donations may not always be reciprocated [23,24]. Smith [4] is doubtful as to the efficacy of this proposal due to the lack of a system of conditional reciprocity linked to meat provisioning. Thus, perhaps counter-intuitively, there is very little clear evidence that the meat produced by hunting is the primary mechanism underpinning the reproductive fitness of hunters. The 'having' theories do not provide adequate explanation.

A third hypothesis, based on Zahavi's "handicap principle" [25], is that hunting success acts as a reliable signal of enviable underlying traits such as athleticism, intelligence or altruism. Successful hunters benefit the community through the provisioning of public goods, an act which enhances their reputation for generosity. The pursuant social standing thereby attained may be attractive to women due to benefits of association such as protection [26]. As such, hunting returns may be exchanged for the future fitness-enhancing benefits of increased social capital or status [27–29]. This theory differs from those previously mentioned in that it need not necessarily be the resource acquisition itself which promotes the reproductive fitness ('having'), but the signal such resourcefulness conveys of underlying male quality ('getting'). The

distribution of acquired meat beyond one's own family unit would also ensure that any such signal was more widely observed [30]. Indeed, hunters are aware that others will know who acquired the meat [31,32]. Male hunting may not then be motivated purely by consequent meat consumption [12,33]. Such signalling would be reliable if it were costly to the signaller, such that an individual lacking in a certain trait would be unable to afford to mimic the signal.

The hypothesis that hunting may act as a signal has been addressed by several authors [30,34,35], but it is as yet unclear what the underlying mechanism may be. In other words, what makes the signal a reliable index of fitness. We first review the physical traits that contribute to hunting success, and then consider potential mechanisms whereby these traits might signal reproductive potential.

Hunting success and physical skills

The hunting of mid-sized animals using hunting technologies such as spears favours a method of disadvantaging or weakening the animal before approaching for the kill. This is because the killing range of spears is very limited, and being close enough to kill a mid-sized animal would be to risk injury to the hunter. Persistence hunting offers such a method, and may be a very effective means of food acquisition under certain conditions. Persistence hunting is a technique by which hunters track and chase prey to the point of prey exhaustion or hyperthermia, often during the hottest part of the day. This technique has been observed in the Kalahari in Africa, and the Tarahumara tribe of Northern Mexico, who have been reported chasing deer until they collapse before strangling them by hand [36,37]. Other animals targeted in this way include steenbok, gemsbok, duiker, caracal, cheetah, kudu and eland [38,39]. During the hunt, chases of up to 35km have been documented. Persistence hunting is useful from the point of view of the early hunter for three reasons; it is relatively low risk, easy for a fit human with animal tracking skills, and requires low metabolic cost relative to potential pay-off [40].

Endurance running may therefore represent a valuable component of hunting success. The evolution of human endurance running ability has attracted attention previously [41,42]. This followed observations that, in comparison with other cursorial animals, humans perform very well over long distances. We are unique amongst primates in possessing the ability to run distances of several kilometres using aerobic metabolism [41], with many amateur human runners able to sustain speeds of 5m/s [40]. This is fast compared with specialised quadrupedal cursors; a dog with a similar mass to a human (65kg) has a trot-gallop transition speed of 3.8m/s, and can then only sustain a gallop for a maximum of 15 minutes under ideal conditions [43]. The same is true of horses, which is surprising as they have been selectively bred for running ability [44]. Human runners can easily cover distances exceeding 10km a day; comparable with hunting dogs and hyenas which run to scavenge and hunt [40]. Consequently, the physical capacity for endurance running appears have been selected for in our genus. Hunting may well have provided the primary selective pressure; evidence for hominin carnivory dates back to approximately 2.5Ma [45]. The ability to run long distances to either hunt or scavenge may have improved the chances of acquiring meat [40,46]. But as described above, if meat was widely shared, how might hunting ability translate into fitness payoffs?

Endurance running might benefit male fitness if it acted as a reliable signal of reproductive potential. Since testosterone is widely associated with reproductive success [47,48], an association between testosterone and endurance running would make running prowess a reliable signal of male reproductive potential. Recent work has reported associations between sporting ability and a marker for foetal testosterone exposure, the 2D:4D ratio [49,50]. This developmental association between testosterone and physical abilities makes it a viable candidate as a signalling mechanism.

The ontogenetic development of digit ratio variability, and significance for reproductive success

The sexually dimorphic digit ratio (2D:4D), first noted by Baker [51], is linked to prenatal androgenisation [52]. The presence of significant sexual dimorphism in the digit ratio of deceased human foetuses suggests 2D:4D ratio is established early in prenatal development [53]. Analysis of amniotic fluid provided direct evidence for a relationship between foetal hormones and digit ratio [54]. This followed indirect reports stemming from homeobox genes [55,56] and congenital adrenal hyperplasia [57,58]. Although the relationship between high digit ratio and prenatal testosterone exposure has been questioned [59], and may be confounded by sexual dimorphism in body size [60], the majority of evidence suggests that digit ratio is a suitable instrument for investigating effects of prenatal androgen exposure on subsequent phenotype [52]. As a result digit ratio is increasingly used as a proxy for foetal hormone environment—to investigate early life predictors of later phenotype, and sex differences therein.

Digit ratio predicts reproductive success in both men and women once the effects of age and population have been removed [61]. Mechanistically, low digit ratios are associated with higher sperm counts and testosterone levels in men, and, conversely, high digit ratios are linked with high oestrogen and luteinising hormone in women [62]. Furthermore, males exhibit a negative relationship between digit ratio and other correlates of reproductive success such as preferred number of children, strength of sex-drive, ease of achieving sexual excitement [47] and sperm numbers per ejaculate [62]. Thus, digit ratio variability emerging early in life has significant implications for fitness.

Digit ratio is negatively correlated with physical prowess across a range of sporting disciplines from slalom skiing [63] to football [64]. Digit ratio has also been tentatively correlated to middle-distance running ability, albeit with a small sample size at distances of less than 4 miles [65]. This study by Manning et al was the first to discuss the relationship between digit ratio and running within the context of persistence hunting. Digit ratio was found to explain a larger portion of the variance in endurance running than expected (up to 25%); explaining more variation than other sports [66] and running over shorter distances [67,68]. As such, the literature supports the view that while 2D:4D does predict running speed, the predictive power increases from sprinting events (1–2%) to events of up to 4 miles in length (20–25%).

We therefore sought to test the hypothesis that physical prowess at endurance running is associated with this putative marker of testosterone exposure. This was performed with a larger sample and distance than previously reported. A female sample was included, as the relationship between female digit ratio and running ability is as yet unknown. Since men undertake the majority of hunting [69], we further predicted that the association between digit ratio and endurance running prowess would be stronger in males than females. Such a sex-difference would suggest that the selective pressure of endurance running has shaped running prowess to be a stronger signal of reproductive potential in males than females. Through such preferences, males would then convert their physical prowess into fitness gains. Our study therefore tests a potential mechanism whereby 'getting' meat could translate into male fitness returns.

Materials and Methods

Athletes (N = 542; m = 439, f = 103) were recruited at the 2013 Robin Hood Half Marathon (21km), held on September 29th. Athletes received an email explaining the study prior to race day, and were invited to take part following the race. Weather conditions were clear skies, with a mean day-time temperature 14°C. The race is a high-profile event, with course records of 61:38 and 73:32 for men and women respectively. Participants ranged between the ages of 19 and 35, and were all Caucasian. The half-marathon distance was chosen due to its

appropriateness to evolutionary hunting-associated running [36]. Race time over 21km was the performance indicator. While this is a measure of speed, the half-marathon distance is considered to be very different from pure speed events such as the 100m sprint in terms of the energy systems utilised. While the 100m sprint utilises the anaerobic system to supply ATP at high rates, prolonged endurance races such as the half-marathon are dependent upon the more sustainable aerobic energy system and lipid metabolism [70–74]. Half-marathons are often used to investigate the effects of endurance exercise on physiology [75–78], so we are confident the event may be used to consider endurance running ability.

All participants participating in the same race, ensuring standardisation of not only distance, but also of time-affecting factors such as weather conditions, time of day and race-course elevation profile. All competitors wore small electronic chips which uniquely identified them as they crossed electronic mats at the start and finish lines, guaranteeing accurate race timings.

Photocopies were taken of athletes' hands upon finishing the race, and measurements of digit ratio were made at a later date. It is appreciated that ratios obtained from photocopies and from direct measurements should not be combined within one study [79], so all measurements were taken from photocopies, with the same machine being used for all copies. This method was chosen due to ease of use and speed in facilitating a large sample size. Digit ratio was measured using Mitutoyo electronic callipers, reading to 0.01mm. Measurements were taken twice from each photocopy to check repeatability. Digit ratios from the first measurement were strongly correlated with the lengths recorded from the second measurement for all individual participants (all $r > 0.95$). In addition, the means of individual right hand and left hand digit ratios were significantly correlated (male $r = 0.88$, $P < 0.001$; female $r = 0.762$, $P < 0.001$). The precision of each measurement was found using the method of Bland & Altman [80]; male right 2D = 2.52; male right 4D = 2.21; male left 2D = 2.36; male left 4D = 2.07; female right 2D = 2.24; female right 4D = 2.04; female left 2D = 1.93; female left 4D = 2.42, all measurements to 2 decimal places. These associations gave confidence in the reliability of the hand-specific measurements of digit ratio, and therefore in the conclusions subsequently drawn.

Ethical approval for the project was granted by the University of Cambridge Human Biology Ethics Committee.

Statistics

Crude associations between digit ratio and race time were explored in each sex using correlation analysis. The difference between the male and female correlation coefficients was analysed using the Fisher r-to-z transformation and subsequent comparison of z-scores [81,82]. Multiple linear regression was used to analyse the sex difference in the relationship between digit ratio and race time. Sex was coded as 0 (female) versus 1 (male), and an 'Interaction' term was constructed by multiplying sex code by digit ratio. Each of sex, 'interaction' and digit ratio were then used as predictors of race time.

Results

Descriptive statistics

A description of the male and females samples is given in Table 1. Males were older, and had significantly lower right and left digit ratios than females.

Among the male subsample there was a significant positive correlation between right and left hand 2D:4D ratio and half-marathon time (right $r = 0.45$, $p < 0.001$; left $r = 0.42$, $p < 0.001$). When age was controlled for the correlation strengthened (right $r = 0.47$, $p < 0.001$; left $r = 0.43$, $p < 0.001$). The same was true among the female subsample (right hand $r = 0.26$, $p < 0.01$; left hand $r = 0.23$, $p = 0.02$), with the correlation strengthening when

Table 1. Descriptive characteristics of the samples.

	Males (n = 439)		Females (n = 103)	
	Mean	SD	Mean	SD
Age (y)	31.7	4.93	28.8	4.58
2D:4D ratio right	0.97	0.033	0.98	0.028
2D:4D ratio left	0.94	0.036	1.01	0.035
Race time (s)	6946	1313	7002	926

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age was controlled for (right $r = 0.29$, $p < 0.01$; left $r = 0.26$, $p < 0.01$). These positive correlations can be seen below in Fig. 1. Note the steeper regression line in the male subsample compared to the female subsample.

Regression analysis revealed that men performed better than women, higher levels of performance were associated with lower digit ratio, and digit ratio increases performance more significantly in men than women ($p<0.05$). Age was not a significant contributor in the regression model, so was removed. See Table 2 for a summary of the results.

Discussion

It was hypothesised that 2D:4D ratio correlates with endurance running performance over the half-marathon distance. This hypothesis has been supported. The male effect sizes are similar to those of Manning et al. [65], which is consistent with the theory that digit ratio explains more variation in endurance running than it does in shorter running events or other sports. The link between digit ratio and maximal oxygen uptake may well relate to these observations [83].

A marker of testosterone exposure is therefore associated with running ability, which ethnographic evidence has shown to be an important attribute for hunting [37]. As testosterone (including the 2D:4D ratio) has been consistently associated with reproductive success [47], this relationship between endurance running ability and digit ratio provides mechanistic evidence in support of the hypothesis that running prowess could act as a reliable signal for male reproductive potential. A conceptual diagram outlining this potential mechanism by which

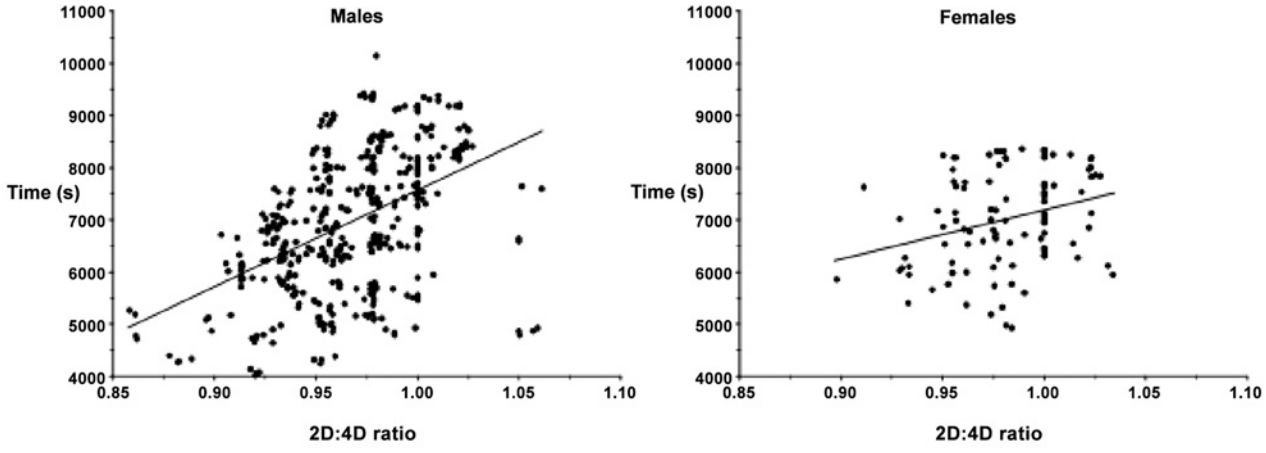


Fig 1. Scatter plot of male and female right hand 2D:4D ratio versus half marathon performance (s). The steeper male gradient is visible.

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Table 2. Regression of half-marathon time in seconds on digit ratio (right in model 1, left in model 2), sex and sex-ratio interaction (right in model 1, left in model 2).

Step	Predictor	β	*t*	*p*
	Model 1			
1	Age	-.057	-1.317	.188
Δ $R2$ = .003, F Change (1,540) = 1.736, p = .188				
2	Age	-.007	-.186	.853
	Sex Code	-2.692	-2.058	.040
	Right Interaction	2.725	2.104	.036
	Right ratio	.249	2.410	.016
Δ $R2$ = .203, F Change (3,537) = 45.692, $p < .001$				
Model summary: F(4,537) = 34.810, $p < 0.001$, $R2$ = .206				
	Model 2			
1	Age	-.057	-1.317	.188
Δ $R2$ = .003, F Change (1,540) = 1.736, p = .188				
2	Age	-.030	-.734	.463
	Sex Code	-2.419	-2.174	.030
	Left Interaction	2.561	2.427	.016
	Left ratio	.248	2.201	.028
Δ $R2$ = .172, F Change (3,537) = 37.239, $p < .001$				
Model summary: F(4,537) = 28.451, $p < 0.001$, $R2$ = .175				

doi:10.1371/journal.pone.0121560.t002

hunting success and running performance could act as a signal of reproductive fitness is given below in Fig. 2.

As a positive relationship between hunting ability and male reproductive success has been reported [2,3], it may be that women are attracted to men with the capacity to 'get', rather than those who 'have'. This may be a consequence of the egalitarian organisation of many forager

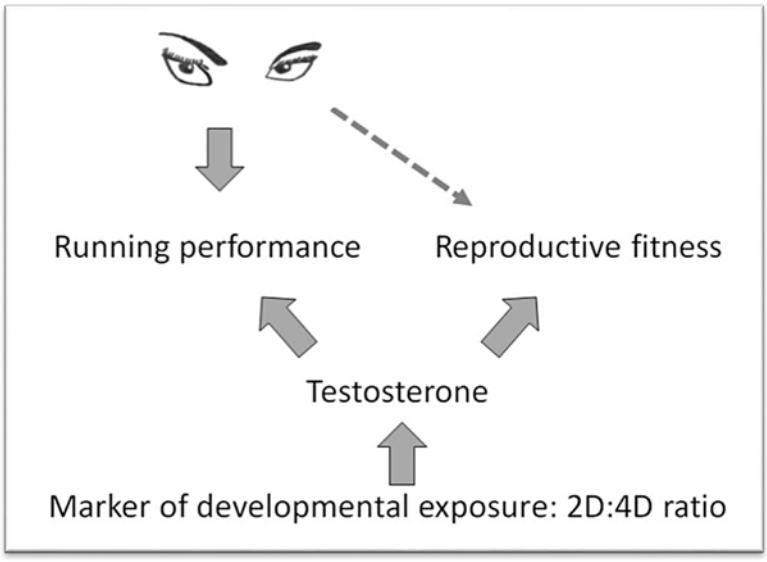


Fig 2. Conceptual diagram outlining a potential mechanism by which hunting success and running performance act as a signal of reproductive fitness.

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societies, which ensures that meat is widely distributed throughout the group [3]. It is acknowledged, however, that this study has not demonstrated that women are in fact differentially attracted to faster male runners, or that this is the only mechanism potentially linking hunting success with reproductive success. Of course, hunting ability and reproductive success may both be correlated with another independent variable which is itself a cause of higher reproductive success, independent of the male's hunting abilities [4].

Although both sexes exhibited a statistically significant positive correlation between right and left hand 2D:4D ratio and time taken to complete a half-marathon running race, the relationship exhibited by males was significantly stronger than that of females. As such, the secondary hypothesis was also supported, suggesting that the ability of running ability to signal reproductive potential has been under stronger selection in males than in females.

Testosterone is not only a link between digit ratio and endurance running ability, but also an important mediator of the male reproductive effort. Behaviourally, testosterone plays an important role in producing sex drive [84] and mediating confidence and assertiveness in social situations [85] – qualities deemed beneficial in the male mating effort. Physiologically, testosterone serves to promote muscle growth [86,87], providing an advantage in male-male combat situations [48,88]. Muscularity is also a sexually attractive trait; more muscular men to report a greater number of sexual partners and younger age at first conception [89,90] and more offspring sired [91].

Muscularity per se, however, could be disadvantageous as a signal of male fitness in a hot environment, as the link between muscle mass and metabolic rate means that a larger muscle mass could induce overheating. Additionally, the high metabolic cost of muscle tissue would not be well suited to environments prone to famine. Running ability may therefore represent a signal of reproductive fitness that is better suited to a hot stochastic environment, where it is furthermore compatible with immediate benefits, given that hunting promotes food acquisition.

Comparative analyses of Olympic winning times and world records has lead some authors to conclude that women will outcompete men in the marathon by the end of the 20th century and over 100m in the mid 22nd century [92,93]. However, caution is required as the initial greater rate of improvement in female performances is most likely due to historical considerations such as the later social acceptance and inclusion of female distance running in major events such as the Olympic Games [94]. The gender difference is now believed to have reached a plateau [95], with the remaining disparity explicable by biological differences between males and females [96]. While it has been suggested that the gender difference in performance disappears as distances increase beyond that of the marathon [97,98], several studies have reported that such distances exhibit no change in relative ability [99]. Indeed, performances between the sexes may even diverge [100,101]. Although it is possible that females improve relative to males with distance, such considerations are not deemed to be relevant to this study as ultra-marathon distances are not applicable to the evolutionary pressures applied by persistence hunting.

To conclude, this investigation has shown that both male and female digit ratios are significantly and negatively correlated to ability in endurance running of a distance/duration comparable with that of persistence hunting (a positive correlation between digit ratio and half marathon time). The relationship was stronger for males than females, suggesting that males faced greater evolutionary pressure to develop endurance running capabilities. We suggest that hunting ability might therefore act as a reliable signal of male fitness, in addition to its function of calorie acquisition. Consequently, the ability to 'get' meat may contribute to the positive relationship between hunting ability and male reproductive success. Our work has used sporting

ability as a proxy for hunting prowess; further work is now required to test this hypothesis in hunting societies.

Author Contributions

Conceived and designed the experiments: DL JTS JCKW. Performed the experiments: DL. Analyzed the data: DL JTS JCKW. Contributed reagents/materials/analysis tools: DL JTS JCKW. Wrote the paper: DL JTS JCKW.

References

1. Buss D. Sex differences in human mate preferences: Evolutionary hypotheses tested in 37 cultures. Behav Brain Sci. 1989; 12(1):1–49.
2. Pennington R, Harpending H. The structure of an African pastoralist community: demography, history, and ecology of the Ngamiland Herero. New York: Oxford Unversity Press; 1993.
3. Kaplan H, Hill K. Food sharing among Ache foragers: Tests of Explanatory Hypotheses. Curr Anthropol. 1985; 26(2):223–46.
4. Smith EA. Why do good hunters have higher reproductive success? Hum Nat. 2004; 15(4):343–64.
5. Pollet T, Nettle D. Driving a hard bargain: sex ratio and male marriage success in a historical US population. Biol Lett. 2008; 4(1):31–3. PMID: 18055406
6. Buunk BP, Dijkstra P, Fetchenhauer D, Kenrick DT. Age and gender differences in mate selection criteria for various involvement levels. Pers Relatsh. 2002; 9(3):271–8.
7. Nettle D, Pollet TV. Natural selection on male wealth in humans. Am Nat. 2008; 172(5):658–66. doi: 10.1086/591690 PMID: 18808363
8. Weissner P, Schiefenövel W, editors. Food and the status quest: an interdisciplinary perspective. Providence, RI: Berghahn Books; 1996.
9. Altman J, Peterson N. Rights to game and rights to cash among contemporary Australian hunter gatherers. 1988.
10. Hill K, Kaplan H. On why male foragers hunt and share food. Curr Anthropol. 1993; 34(5):701–10.
11. Kaplan H, Hill K. Hunting ability success among male Ache foragers: Preliminary research conclusions. Curr Anthropol. 1985; 26(1):131–3.
12. Hawkes K, O'Connell JF, Blurton Jones N. Hunting and nuclear families some lessons from the Hadza about men's work. Curr Anthropol. 2001; 42(5):681–709.
13. Hawkes K. On why male foragers hunt and share food: reply to Hill and Kaplan. Curr Anthropol. 1993; 345:706–10.
14. Trumble BC, Smith EA, Connor KAO, Kaplan HS, Gurven MD. Successful hunting increases testosterone and cortisol in a subsistence population. Proc R Soc B Biol Sci. 2013; 281(1776).
15. Sugiyama L, Chacon R. Effects of illness and injury on foraging among the Yora and Shiwiar: pathology risk as adaptive problem. Human behavior and adaptation: an anthropological perspective. 2000. p. 371–95.
16. Patton J. Coalitional effects on reciprocal fairness in the ultimatum game: A case from the Ecuadorian Amazon. Foundations of human sociality: Economic experiments and ethnographic evidence from fifteen smallscale societies. 2004. p. 96–124.
17. Patton J. Meat sharing for coalitional support. Evol Hum Behav. 2005; 26(2):137–57.
18. Hawkes K, Altman J, Beckerman S, Grinker R, Jeske R, Peterson N, et al. Why gatherers work; An ancient version of the problem of public goods. Curr Anthropol. 1993; 34(4):341–61.
19. Lee R, DeVore I. Problems in the study of hunters and gatherers. Man the Hunter. 1968. p. 3–12.
20. Enloe JG. Food sharing past and present: archaeological evidence for economic and social interactions. Before Farming. 2003; 1.1:1–23.
21. Trivers R. The evolution of reciprocal altruism. Q Rev Biol. 1971;35–57.
22. Kishigami N. Contemporary Inuit food sharing and hunter support program of Nunavik, Canada. Senri Ethnol Stud. 2000; 53:171–92.
23. Tucker VA. The energetic cost of moving about: walking and running are extremely inefficient forms of locmotion. Much greater efficiency is achieved by birds, fish-and bicyclists. Am Sci. 1975; 63(4):413–9. PMID: 1137237

24. Bliege Bird R, Bird DW, Smith EA, Kushnick GC. Risk and reciprocity in Meriam food sharing. Evol Hum Behav. 2002; 23(4):297–321.
25. Zahavi A. Mate selection—a selection for a handicap. J Theor Biol. 1975; 53:205–14. PMID: 1195756
26. Blurton Jones N, Marlowe F, Hawkes K, O'Connell JF. Hunter-gatherer divorce rates and the paternal provisioning theory of human monogamy. In: Cronk L, Chagnon N, Irons W, editors. Adaptation and human behaviour: an anthropological perspective. New York, NY: Aldine de Gruyter; 2000. p. 65–84.
27. Bliege Bird R, Smith EA. Signaling theory, strategic interaction, and symbolic capital. Curr Anthropol. 2005; 46(2):221–48.
28. Gurven M, Allen-Arave W, Hill K, Hurtado M. "It's a wonderful life". signaling generosity among the Ache of Paraguay. Evol Hum Behav. 2000; 21(4):263–82. PMID: 10899478
29. Bliege Bird R, Scelza B, Bird DW, Smith EA. The hierarchy of virtue: mutualism, altruism and signaling in Martu women's cooperative hunting. Evol Hum Behav. Elsevier Inc.; 2012; 33(1):64–78.
30. Smith EA, Bliege Bird R. Turtle hunting and tombstone opening: public generosity as costly signaling. Evol Hum Behav. 2000; 21(4):245–61. PMID: 10899477
31. Hawkes K. Showing off: tests of a hypothesis about men's foraging goals. Ethol Sociobiol. 1991; 12-(1):29–54.
32. Hawkes K. Sharing and collective action. Evolutionary ecology and human behavior. In: Smith E, Winterhalder B, editors. Evolutionary Ecology and human behaviour. Hawthorne, NY: de Gruyter; 1992. p. 269–300.
33. Bliege Bird R, Smith E, Bird D. The hunting handicap: costly signaling in human foraging strategies. Behav Ecol Sociobiol. 2001; 50(1):9–19.
34. Hawkes K, Bliege Bird R. Showing off, handicap signaling, and the evolution of men's work. Evol Anthropol Issues, News, Rev. 2002; 11(2):58–67.
35. Hawkes K. Why do men hunt? Some benefits for risky strategies. In: Cashdan E, editor. Risk and uncertainty in tribal and peasant economies. Boulder: Westview Press; 1990. p. 145–66.
36. Pennington C. The Tarahumara of Mexico. Salt Lake City: University of Utah Press; 1963.
37. Liebenberg L. Persistence hunting by modern hunter gatherers. Curr Anthropol. 2006; 47(6):1017–26.
38. Steyn H. Southern Kalahari San subsistence ecology: A reconstruction. South African Archaeol Bull. 1984;117–24.
39. Schapera I. The Khoisan Peoples of South Africa: Bushmen and Hottentots. London: Routledge and Kegan Paul; 1930.
40. Lieberman DE, Bramble DM, Raichlen DA, Shea JJ. Brains, brawn, and the evolution of human endurance running capabilities. In: Grine, Fleagle, Richard, Leakey, editors. The First Humans—Origin and Early Evolution of the Genus Homo. Springer; 2006.
41. Carrier DR. The energetic paradox of human running and hominid evolution. Curr Anthropol. 1984; 25 (4):483–95.
42. McDougall C. Born to Run: A hidden tribe, superathletes, and the greatest race the world has ever seen. Knopf; 2009.
43. Heglund N, Taylor C. Speed, stride frequency and energy cost per stride: how do they change with body size and gait? J Exp Biol. 1988; 138:301–18. PMID: 3193059
44. Minetti AE. Efficiency of equine express postal systems. Nature. 2003; 426:785–6. PMID: 14685222
45. Semaw S, Renne P, Harris J, Feibel C, Bernor R, Fesseha N, et al. 2.5-million-year-old stone tools from Gona, Ethiopia. Nature. 1997; 385:333–6. PMID: 9002516
46. Bunn H. Hunting, power scavenging, and butchering by Hadza foragers and by Plio-Pleistocene Homo. Meat-eating and human evolution. 2001.
47. Manning JT, Fink B. Digit ratio (2D:4D), dominance, reproductive success, asymmetry, and sociosexuality in the BBC Internet Study. Am J Hum Biol. 2008; 20(4):451–61. doi: 10.1002/ajhb.20767 PMID: 18433004
48. Bribiescas R. Reproductive physiology of the human male. Reproductive ecology and human evolution. 2001. p. 107–33.
49. Pokrywka L, Rachoń D, Suchecka-Rachoń K, Bitel L. The second to fourth digit ratio in elite and non-elite female athletes. Am J Hum Biol. 2005; 17(6):796–800. PMID: 16254897
50. Paul S, Kato B, Hunkin J, Vivekanandan S, Spector T. The big finger: the second to fourth digit ratio is a predictor of sporting ability in women. Br J Sports Med. 2006; 40(12):981–3. PMID: 17008344
51. Baker F. Anthropological Notes on the Human. Am Anthropol. 1888; 1(1):51–76.

52. Hönekopp J, Bartholdt L, Beier L, Liebert A. Second to fourth digit length ratio (2D:4D) and adult sex hormone levels: new data and a meta-analytic review. Psychoneuroendocrinology. 2007; 32(4):313–21. PMID: 17400395

53. Galis F, Ten Broek CMA, Van Dongen S, Wijnaendts LCD. Sexual dimorphism in the prenatal digit ratio (2D:4D). Arch Sex Behav. 2010; 39(1):57–62. doi: 10.1007/s10508-009-9485-7 PMID: 19301112

54. Lutchmaya S, Baron-Cohen S, Raggatt P, Knickmeyer R, Manning JT. 2nd To 4th digit ratios, fetal testosterone and estradiol. Early Hum Dev. 2004 Apr; 77(1–2):23–8. PMID: 15113633

55. Kondo T, Zákány J, Innis JW, Duboule D. Of fingers, toes and penises. Nature. 1997; 390(6655):29. PMID: 9363887

56. Mortlock D, Innis J. Mutation of HOXA13 in hand-foot-genital syndrome. Nat Genet. 1997; 15(2):179–80. PMID: 9020844

57. Brown WM, Hines M, Fane BA, Breedlove SM. Masculinized finger length patterns in human males and females with congenital adrenal hyperplasia. Horm Behav. 2002; 42(4):380–6. PMID: 12488105

58. Okten A, Kalyoncu M, Yariş N. The ratio of second- and fourth-digit lengths and congenital adrenal hyperplasia due to 21-hydroxylase deficiency. Early Hum Dev. 2002; 70(1–2):47–54. PMID: 12441205

59. Berenbaum SA, Bryk KK, Nowak N, Quigley CA, Moffat S. Fingers as a marker of prenatal androgen exposure. Endocrinology. 2009; 150(11):5119–24. doi: 10.1210/en.2009-0774 PMID: 19819951

60. Kratochvíl L, Flegr J. Differences in the 2nd to 4th digit length ratio in humans reflect shifts along the common allometric line. Biol Lett. 2009; 5(5):643–6. doi: 10.1098/rsbl.2009.0346 PMID: 19553247

61. Manning JT, Barley L, Walton J, Lewis-Jones D, Trivers RL. The 2nd: 4th digit ratio, sexual dimorphism, population differences, and reproductive success: evidence for sexually antagonistic genes? Evol Hum Behav. 2000; 21:163–83. PMID: 10828555

62. Manning J, Scutt D, Wilson J, Lewis-Jones D. The ratio of 2nd to 4th digit length: a predictor of sperm numbers and concentrations of testosterone, luteinizing hormone and oestrogen. Hum Reprod. 1998; 13(11):3000–4. PMID: 9853845

63. Manning J. The ratio of the 2nd to 4th digit length and performance in skiing. J Sports Med Phys Fitness. 2002; 42(4):446. PMID: 12391439

64. Manning JT, Taylor RP. Second to fourth digit ratio and male ability in sport: implications for sexual selection in humans. Evol Hum Behav. 2001; 22(1):61–9. PMID: 11182575

65. Manning J, Morris L, Caswell N. Endurance running and digit ratio (2D: 4D): Implications for fetal testosterone effects on running speed and vascular health. Am J Hum Biol. 2007; 421:416–21.

66. Hönekopp J, Schuster M. A meta-analysis on 2D:4D and athletic prowess: Substantial relationships but neither hand out-predicts the other. Pers Individ Dif. 2010 Jan; 48(1):4–10.

67. Manning J, Hill M. Digit ratio (2D:4D) and sprinting speed in boys. Am J Hum Biol. 2009; 21(2):210–3. doi: 10.1002/ajhb.20855 PMID: 19107924

68. Trivers R, Hopp R, Manning J. A longitudinal study of digit ratio (2D:4D) and its relationship with adult running speed in Jamaicans. Hum Biol. 2013; 85(4):623–6. PMID: 25019194

69. Biesele M, Barclay S. Ju/'huan women's tracking knowledge and its contribution to their husbands' hunting success. African Study Monogr. 2001; 26:67–84.

70. Duffield R, Dawson B, Goodman C. Energy system contribution to 100-m and 200-m track running events. J Sci Med Sport. 2004; 7(3):302–13. PMID: 15518295

71. Hagerman F. Energy metabolism and fuel utilization. Med Sci Sport Exerc. 1992; 24(9 Supple):S309–14.

72. Wilmore J, Costill D. Physiology of sport and exercise. 2nd ed. Human Kinetics Publishers; 1999.

73. Brooks GA, Mercier J. Balance of carbohydrate and lipid utilization during exercise: the "crossover" concept. J Appl Physiol. 1994; 76(6):2253–61. PMID: 7928844

74. McArdle W, Katch F, Katch V. Exercise physiology: energy, nutrition and human performance. Philadelphia, PA: Lippincott, Williams & Wilkins; 2001.

75. Dalla Vecchia L, Traversi E, Porta A, Lucini D, Pagani M. On site assessment of cardiac function and neural regulation in amateur half marathon runners. Open Hear. 2014; 1(1):e000005.

76. Oomah S, Mousavi N, Bhullar N, Kumar K, Walker J, Lytwyn M, et al. (2011). The role of three-dimensional echocardiography in the assessment of right ventricular dysfunction after a half marathon: comparison with cardiac magnetic resonance imaging. J Am Soc Echocardiogr. 2011; 24 (2):207–13. doi: 10.1016/j.echo.2010.10.012 PMID: 21281911

77. Lippi G, Longo UG, Maffulli N. Genetics and sports. Br Med Bull [Internet]. 2010; 93:27–47.

78. Dion T, Savoie F, Asselin A, Gariepy C, Goulet E. Half-marathon running performance is not improved by a rate of fluid intake above that dictated by thirst sensation in trained distance runners. Eur J Appl Physiol. 2013; 113(12):3011–20. doi: 10.1007/s00421-013-2730-8 PMID: 24085484

79. Manning JT, Fink B, Neave N, Caswell N. Photocopies yield lower digit ratios (2D:4D) than direct finger measurements. Arch Sex Behav [Internet]. 2005; 34(3):329–33. PMID: 15971015

80. Bland JM, Altman DG. Statistical methods for assessing agreement between two methods of clinical measurement. Lancet. 1986; 307:1–9.

81. Preacher K. Calculation for the test of the difference between two independent correlation coefficients [Computer software].

82. Cohen J, Cohen P. Applied multiple regression/correlation analysis for the behavioral sciences. Hillsdale, New Jersey: Erlbaum; 1983.

83. Hill R, Simpson B, Millet G, Manning J, Kilduff L. Right-left digit ratio (2D:4D) and maximal oxygen uptake. J Sports Sci. 2011; 30(2):129–34. doi: 10.1080/02640414.2011.637947 PMID: 22141747

84. Baumeister RF, Catanese KR, Vohs KD. Is there a gender difference in strength of sex drive? theoretical views, conceptual distinctions, and a review of relevant evidence. Personal Soc Psychol Rev. 2001 Aug; 5(3):242–73.

85. Ellison P. Energetics and reproductive effort. Am J Hum Biol. 2003; 15:342–51. PMID: 12704710

86. Griggs R, Kingston W, Jozefowicz R, Herr B, Forbes G, Halliday D. Effect of testosterone on muscle mass and muscle protein synthesis. J Appl Physiol. 1989; 66:498–503. PMID: 2917954

87. Kadi F. Cellular and molecular mechanisms responsible for the action of testosterone on human skeletal muscle. A basis for illegal performance enhancement. Br J Pharmacol. 2008; 154(3):522–8. doi: 10.1038/bjp.2008.118 PMID: 18414389

88. Dijkstra P, Buunk BP. Sex differences in the jealousy-evoking effect of rival characteristics. Eur J Soc Psychol. 2002; 32(6):829–52.

89. Frederick DA, Haselton MG. Why is muscularity sexy? Tests of the fitness indicator hypothesis. Pers Soc Psychol Bull. 2007; 33(8):1167–83. PMID: 17578932

90. Gallup AC, White DD, Gallup GG. Handgrip strength predicts sexual behavior, body morphology, and aggression in male college students. Evol Hum Behav. 2007; 28(6):423–9.

91. Wells J, Charoensiriwath S, Treleaven P. Reproduction, aging, and body shape by three-dimensional photonic scanning in Thai men and women. Am J Hum Biol. 2011; 23(3):291–8. doi: 10.1002/ajhb.21151 PMID: 21387458

92. Whipp B, Ward S. Will women soon outrun men? Nature. 1992; 355(6355):25. PMID: 1731197

93. Tatem A, Guerra C, Atkinson P, Hay S. Momentous sprint at the 2156 Olympics? Nature. 2004; 431 (7008):525–6. PMID: 15457249

94. Noakes T. Lore of running. Champagn, Illinois: Leisure Press; 2003.

95. Sparling P, O'Donnell E, Snow T. The gender difference in distance running performances has plateaued: an analysis of world rankings from 1980 to 1996. Med Sci Sport Exerc. 1998; 30(12):1725–9. PMID: 9861606

96. Cheuvront SN, Carter R, Deruisseau KC, Moffatt RJ. Running performance differences between men and women:an update. Sports Med. 2005; 35(12):1017–24. PMID: 16336006

97. Bam J, Noakes T, Juritz J, Dennis S. Could women outrun men in ultramarathon races? Med Sci Sport Exerc. 1997; 29(2):244–7. PMID: 9044230

98. Speechly D, Taylor S, Rogers G. Differences in ultra-endurance exercise in performance-matched male and female runners. Med Sci Sport Exerc. 1996; 28(3):359–65. PMID: 8776224

99. Hoffman M. Ultramarathon trail running comparison of performance-matched men andwomen. Med Sci Sport Exerc. 2008; 40(9):2008.

100. Coast J, Blevins J, Wilson B. Do gender differences in running performance disappear with distance? Can J Appl Physiol. 2004; 29(2):139–245. PMID: 15064423

101. Eichenberger E, Knechtle B, Rüst CA, Rosemann T, Lepers R. Age and sex interactions in mountain ultramarathon running—the Swiss Alpine Marathon. Open access J Sport Med. 2012; 3:73–80. doi: 10.2147/OAJSM.S33836 PMID: 24198590