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## DO ELITE TENNIS PLAYERS SHOW SEX-SPECIFIC SENESCENT DECLINES?

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### ABSTRACT

Aging is characterized by rising mortality, declining fertility and declines in physiological function (functional senescence). Sex-differences in the tempo and severity of survival and fertility declines are widespread, but it is less clear how often, and how much, trajectories of functional senescence diverge between the sexes. We test how physiological function changes with age in male and female elite tennis players using first-serve speed (power) and first-serve accuracy as performance measures. We find absolute differences between the sexes with men serving more quickly, but less accurately, than women. Both power and accuracy showed senescent declines but these began earlier for power. There were signals of trait-compensation, where players with pronounced power declines showed increases in accuracy, which might partially buffer against power deterioration. However, there were no sex differences in how either trait changed with age, contrasting with other sports. Sex differences in functional senescence are probably shaped by interactions between natural and sexual selection, the proximate costs of trait expression and a trait's genetic architecture, and so are highly trait-specific. Given that elite athletes are outliers with respect to human physical abilities, this may not be the right demographic for disentangling these complex interactions.

**KEY-WORDS:** Aging, Functional Senescence, Sexual Selection, Sport, Tennis

## INTRODUCTION

Aging is characterized by declining fertility and rising mortality over age (Baudisch and Vaupel 2012). However, growing older is also accompanied by physiological declines. Older humans have reduced cognitive ability (Bishop *et al.* 2010), muscle mass (Nair 2005) and immune function (Bupp 2015). These declines, referred to as functional senescence, may reduce the happiness and well-being of the elderly (Angner *et al.* 2009). Functional senescence also explains why aging female orb web spiders weave lower quality webs and take longer to catch prey (Anotaux *et al.* 2014) and why older great tits produce less consistent songs, which may reduce how well males hold territories or attract mates (Rivera-Gutierrez *et al.* 2012). Although functional senescence can reduce evolutionary fitness, aging research tends to focus more on changing mortality and fertility than on age-associated functional declines (Grotewiel *et al.* 2005; Petrosyan *et al.* 2014; Reichard 2017).

Traditionally, functional senescence was thought to involve a general loss of function, with multiple traits declining in synchrony as selection weakens with age (Williams 1957). However, this is not the case and different traits often lose function at different rates (Herndon *et al.* 2002; Burger and Promislow 2006; Nussey *et al.* 2009; Lailvaux *et al.* 2011; Rivera-Gutierrez *et al.* 2012; Lailvaux *et al.* 2014). This may be because some traits are less costly to maintain than others, which might explain why male red deer keep producing antlers as they grow older but show severe declines in rutting performance - it is easier for old deer to create antlers, than to allocate energy towards rutting (Nussey *et al.* 2009). There may also be variation in the strength of selection acting on particular traits (Burger and Promislow 2006). Although aging is ultimately due to declining selection over age (Hamilton 1966; Wensink *et al.* 2017), if a trait is under particularly strong selection it may pay to continue investing in it, thereby preserving its function even if this comes at the expense of other characters (Burger and Promislow 2006). These same drivers of variation in trait-specific functional decline (*i.e.* different proximate costs, and variation in the strength of age-dependent selection) may also explain why patterns of functional decline can differ between the sexes.

Sex differences in demographic measures of aging are widespread (Tidière *et al.* 2015), but sex differences are also seen in functional measures of aging. For example, changes in bite force and jumping ability with age are sex-specific in field crickets (Lailvaux *et al.* 2011), female rhesus monkeys maintain motor function better than males as they grow older (Lacreuse *et al.* 2005), and *Drosophila* survival after infection depends on an interaction between sex, age and infection route (Kubiak and Tinsley 2017). Although sex-specific patterns of functional senescence are common, they are not universal. Male and female roe deer show similar senescent declines in immune function (Cheynel *et al.* 2017), while physical strength declines in a similar way in aging male and female grey mouse lemurs (Hämäläinen *et al.* 2015). In humans however, there are clear signals of sex-specific trajectories of functional declines, as elderly women are more likely to experience greater restrictions in their daily living than age-matched men (Oksuzyan *et al.* 2008; Oksuzyan *et al.* 2014; Bastos *et al.*

2015; Austad and Fischer 2016). However, because our understanding of sex differences in human functional senescence is largely derived from the elderly, it is unclear how frequently trait specific trajectories of functional declines diverge in men and women, and when this divergence occurs.

If there are sex differences in the tempo or severity of functional declines, we might see differences in how males and females compensate for functional deterioration (Lailvaux *et al.* 2014). When performing complex behaviors, such as running, leaping or foraging, individuals must coordinate a range of actions and if there are senescent declines in one component of that behavior, these may be counteracted by increases elsewhere. For example, an aging predator that loses muscle mass may compensate for this decline by relying more heavily on stealth, thereby preserving overall hunting success. This may explain why Ache men's hunting success peaks after they have started to experience declines in strength - successful hunting requires skills that take years to attain, which can compensate for age-associated losses in strength, speed or power (Walker *et al.* 2002). Sex-specific functional declines and dynamic compensation for them may mean that we see very different patterns of functional change in correlated traits in men and women. This idea has not been tested comprehensively, but performance data in elite athletes may help us identify sex-specific performance declines and compensation (Lailvaux *et al.* (2014).

Data on athletes are considered to be excellent for aging research because differences in motivation between athletes engaged in high level competition are unlikely, performance data are collected in a uniform environment, and reductions in exercise levels over age and associated changes in body composition are likely to be uniformly low (Tanaka and Seals 2003). This means that any age-associated changes in performance in elite athletes are likely to represent aging rather than behavior or lifestyle changes. Athletes must also integrate perceptual, cognitive and motor skills to excel in their sports, and good technique, strength and speed may all be vital to an athlete's success. This integration of multiple physical traits means that there is scope to study trait compensation and compare patterns of change in correlated traits across the sexes. Lailvaux and colleagues (2014) did this and found patterns suggesting that in professional basketball players, men, but not women, experience pronounced performance declines over age. However, these datasets for men and women differed in collection period, sample size, and average length of careers, perhaps limiting their usefulness for direct comparisons between the sexes. The traits analyzed by Lailvaux and colleagues (2014) were points scored by players in different areas of the court with, or without interference from opponents. These measures integrate multiple physical attributes including agility, strength, power and accuracy, which makes them excellent measures of overall performance, but makes it hard to discuss what each trait tells us about the broader physiology of any declines. Finally, basketball is a team sport, and it may be more appropriate to analyze functional changes in sports where we can better decouple an individual's performance from that of their team and opposition.

With this in mind, we characterize functional declines in a sport where each athlete competes individually, using performance measures that have little scope for being directly affected by the

opposition and that have clear biological interpretations. We characterize sex-specific patterns of aging in average speed of the first serve (a measure of power) and in the proportion of first serves that were in play (a measure of accuracy) in the top 100 all-time highest earning male and female tennis professionals. This allows us to broaden our understanding of sex-specific functional declines and to test for dynamic trait compensation where declines in one aspect of serve quality are compensated for by improvements in a second.

## METHODS

### *Data*

We collected data from [www.OnCourt.info](http://www.OnCourt.info), a publicly available database containing statistical information on professional tennis players and tournaments. We used data on male and female professional tennis players who currently participate, or have participated, in either the ATP (Association of Tennis Professionals) or WTA (Women's Tennis Association) tours. We collected data from the top-100 highest-earning players from both the men's and women's tours. Because prize money reflects how far players progress in tournaments, studying the highest-earning players standardizes the ability of athletes – all players are of exceptionally high caliber. This should minimize selective disappearance where low quality members of a cohort disappear earlier than high quality players. Our subset does not result in 100 male and female players because some of the top-100 all-time highest earners retired before serve data started being recorded sufficiently accurately (see below), and therefore could not be used in this study.

We compiled serve data for each Grand Slam match that individual tennis players played throughout their career, during the period for which sufficiently high quality data were collected in this database. We only collected data from Grand Slam tournaments (Australian Open, Roland-Garros, Wimbledon and the U.S. Open) because these are the only competitions where high-quality serve data appears in this database. Our dataset is taken from the years 2003–2017: 2003 is the first year that serve data started being collected and digitized. This means that some players only feature in the data from relatively advanced ages because they were nearing retirement at 2003, while some players in the database are still active in the game today. These data therefore follow some players throughout their entire Grand Slam career, while we only capture snapshots of the career for other players. Ultimately, this meant we obtained data for 74 male players totaling 4,461 individual matches, and 84 female players with a total of 4,815 matches.

We collected data on player age, sex, their first serve percentage and average first serve speed for each match played. First serve percentage is the percentage of playable serves i.e. those that fell within the appropriate region of the court, and is therefore a measure of serve accuracy. The average first serve speed is our proxy of serve power. These two traits have clear interpretations (accuracy and power) and to perform a high quality serve, players need to integrate both traits. This means that we

can look for trait compensation to see if reductions in one character over age are compensated by improvements in the other. It is worth noting that tennis players have the opportunity to serve twice for each point played. If the first shot is not valid, they may make a second attempt. We study the first serve because it often leads to a direct point (an ace or unreturned serve) and players try to maximise speed and accuracy to win a point. In contrast, the second serve is played with less speed to have greater security: if players miss the second serve, they lose the point. We thus deemed it a less appropriate trait for analyses.

### ***Statistical analyses***

We fitted linear mixed effect models in R version 3.4.2 (R Core Development Team 2017) using the function *lmer* implemented in *lme4* (Bates et al. 2014). Visual inspection of residuals from fitted models suggested both serve speed and accuracy conformed to the assumption of residual normality and homoscedasticity. For both response variables serve speed and serve accuracy, our full models included linear and quadratic effects of player age and their interaction with sex as fixed effects. Men's matches can last for up to five sets, whereas women play a maximum of three sets, and the length of a match may influence average serve speed and accuracy. In our dataset, women's matches lasted on average 2.3 sets and men's lasted 3.6 sets. To rule out that sex differences are driven by differences in match length, we included the number of sets played as an additional fixed effect. We included random intercepts as well as random linear and quadratic slopes over age for individual players to account for pseudo-replication in estimating aging patterns (Schielzeth and Forstmeier 2008), as well as random intercepts for tournament (factor with four levels) and year (factor with 14 levels) to account for variable environments (e.g. court surface and climate) as well as for temporal variation. To aid the interpretation of main effects in the presence of interactions (Schielzeth 2010), player age and number of sets played were standardized by mean-centering and scaling to 1SD, and sex was centered by assigning females and males values of -0.5 and 0.5, respectively. We obtained statistical significance of fixed effects with likelihood ratio tests (LRTs), using  $\chi^2$  tests on twice the difference in model log likelihoods, with the number of degrees of freedom equal to the number of additional parameters in the more complex model. Non-significant terms were sequentially removed to derive minimal adequate models, starting with higher-order interactions and quadratic terms. We extracted model parameters from minimal adequate models and calculated approximate 95% confidence intervals by multiplying Student's t-values for given sample sizes (number of players) by the standard errors of the effect sizes (Crawley 2012). To check whether removal of non-significant terms biased effect sizes (Forstmeier and Schielzeth 2011), we compared estimates from our minimal adequate models with estimates from full models.

To investigate among-individual variances and co-variances between traits, and to explore how serve speed and accuracy might influence winning matches, we fitted tri-variate models using a Bayesian approach implemented in *MCMCglmm* (Hadfield 2010 and see Supplementary Information).

Briefly, we included fixed effects identified as important during univariate model selection, random effects were included as described above, but we omitted random quadratic slopes to reduce autocorrelation. We verified model convergence, absence of autocorrelation, and robustness to prior specification. Means and credible intervals for among-match and among-individual correlations between traits were estimated from (co)variances. To visualize correlations, we used best linear unbiased predictors (BLUPs) and random slope estimates (Houslay and Wilson 2017).

## RESULTS

### *Data summary*

Our dataset contained performance data for women aged 15 to 47, and for men aged 17 to 38 years (Fig S1). The average number of years players were active in the database was 8.7 for men and 8.1 for women. After the age of 38, only 2 women remained in the game and so these data do not suggest that women keep playing at an elite level for longer than men. However, our database contained 33 women who were playing at elite level aged 18, in contrast to only 11 men. This might suggest that women begin their Grand Slam career earlier than men.

### *Functional Declines*

Trajectories of functional changes for the traits we studied varied enormously between individual players, with some players showing age-dependent declines in performance, while others show pronounced improvements. On average, serve speed differed across the sexes, with men serving faster than women (Fig 1, Table 1), although there was considerable overlap between the sexes. A negative quadratic effect of age showed that serve speed peaked at intermediate ages, while the linear effect of age was not significantly different from zero, indicating that serve speed did not show an overall increase or decrease with age but peaked at the mean age of 26 years. Importantly, neither the linear nor the non-linear effects of age differed across the sexes (Table 1) showing that the trajectory of declines in serve speed were similar across the sexes.

We found different patterns for serve accuracy (Fig 2, Table 1). Here, female players served more accurately than male players, and accuracy was affected by a positive linear and a negative quadratic effect of age. The quadratic term indicates a peak in serve accuracy, where initial improvements are followed by a decline. However, the positive linear term suggested an increase in serve accuracy over age (Fig 2). This positive linear effect of age reflects that the peak in serve accuracy is later than the mean age, i.e. around the age of 28 years. Thus, serve accuracy peaks a little later in life than serve speed. Again, there was no evidence for sex differences in aging patterns (Table 1).

Longer matches with more sets played were significantly associated with slower but more accurate serves (Table 1). Controlling for the number of sets played thus allowed us to estimate minimally confounded sex differences in serve speed and accuracy.

### ***Trade-offs and Trait Compensation***

Winning a match was positively (albeit weakly) associated with serve speed and accuracy (correlations [credible intervals] calculated from trait (co)variances: speed 0.05 [0.002, 0.10], accuracy 0.13 [0.09, 0.18]). When considering among-individual covariation between serve traits and winning (color gradient in Fig 3a), and between the aging trajectories of the traits (color gradient in Fig 3d), we found positive correlations both for individual-level intercepts (Fig 3b) and for individual-level slopes (Fig 3c), although the credible intervals overlapped zero for two of the four pairwise correlations.

In an ideal world, players would make very accurate and very fast serves. However, we found evidence of a trade-off between serve speed and serve accuracy at multiple levels. On a match level, matches with higher average first serve speed showed lower first serve accuracy (among-match between-trait correlation: -0.29 [-0.31, -0.27]). Among players, after accounting for age-associated variation and for absolute differences between men and women, there was a negative association between serve speed and serve accuracy in both males and females (among-individual between-trait correlation: -0.37 [-0.49, -0.20]; Fig 3a). Finally, across the sexes, men had faster but less accurate serves than women.

Where players lay on the axes between very fast, less accurate serves and very accurate, slow serves changed over their career. Players with a stronger than average decline in serve speed showed the most pronounced increase in serve accuracy and vice versa (i.e., there was a negative correlation between players' random slopes for speed and accuracy: -0.57 [-0.72, -0.38]; Fig 3d). The outcome of this is that as serve speed declines, increases in accuracy can buffer against these declines to help preserve serve quality. This hints at trait-compensation. However, we note that the quadratic components of aging were negative for both traits, meaning that on average in our population, trait compensation was incomplete.

## **DISCUSSION**

To explore sex differences in human functional senescence, as well as patterns of dynamic compensation for these declines, we analysed two indicators of performance in elite tennis players (first serve speed and accuracy) and asked how these traits change as players age. We found clear sex differences in each trait, with men serving faster but less accurately than women. This pattern was in line with an underlying trade-off between serve speed and accuracy, which manifested at different levels. Over age, both traits showed clear performance peaks, rising and then declining as players aged, but declines began later for serve accuracy than serve speed. We also found that players with pronounced declines in serve speed over age showed increases in serve accuracy. This suggests that there is scope for compensating for senescent declines in serve power by improving serve accuracy. However, given that on average in our population both speed and accuracy decline in older players,

this trait compensation must be incomplete. Contrary to our expectations, age-dependent changes were similar in women and men.

There were absolute sex differences in both serve traits as on average, men served faster than women at all ages, although there was considerable overlap between the sexes (Fig 1). How quickly players serve depends on the speed of internal rotation along the pelvis, torso and shoulder, and faster serves in men have been attributed to greater internal rotation strength (Fleisig *et al.* 2003). Arm length may also play a role in serve speed, as in cricket and baseball, players with longer arms typically bowl faster (Pyne *et al.* 2006). On balance, greater height and muscle mass in men explains their faster serves. While strength may have fitness benefits to both sexes, helping men hunt game (Apicella 2014) and women retrieve foraged foods (Hawkes *et al.* 1989), natural selection on height and strength may be particularly strong in men. For example, taller people are perceived as being more dominant, but this effect is stronger in men than women (Blaker *et al.* 2013). Height and strength may also be under strong sexual selection in males, helping men attract mates (Pawlowski *et al.* 2000; Frederick and Haselton 2007; Stulp *et al.* 2013) and outcompete rivals (Sell *et al.* 2009), and sexual competition was a key determinant of male reproductive success in our evolutionary history (Puts 2010). A history of particularly strong natural and sexual selection on male height and musculature, may underpin the faster serves seen in male tennis players.

While men typically serve faster than women, women's serves were more often on target (Fig 2). This reflects a trade-off between serving very fast and serving very accurately (Fig 3a). This trade-off is not surprising given that, in general, as the velocity of movement to a target increases, the accuracy of movement to the target declines (Fitts 1954). Similar trade-offs have been observed in other sports including darts (Etnyre 1998; Edwards *et al.* 2007), badminton (Edwards *et al.* 2005) and football (Timmis *et al.* 2014). However, the magnitude of this trade-off can vary as a function of experience. For example, advanced handball players can increase throwing speed without reducing throw accuracy, while novices cannot (García *et al.* 2013). Previous data on tennis players suggested that there is no trade-off between return shot speed and accuracy (Landlinger *et al.* 2012) or serve speed and accuracy (Cauraugh *et al.* 1990). However, these studies lacked the power of the current dataset; the former considered 13 and 15 players respectively, while ours considers 170 players and multiple matches per player.

Both of the traits we analyzed showed age-associated changes: performance improved, peaked and then declined over age. For serve speed, these changes in performance were relatively symmetrical around the sex-specific mean. That is, serve speed peaked in players of average age, and declines were symmetrical on either side of this peak. The decline in older players reflects senescence. This is not surprising given that muscle function, which is likely to affect serve speed, begins to decline in our fourth decade (Nair 2005). In healthy adults taken from the general population this decline in muscle function does not result in decreased strength until participants reach their forties (Bäckman *et al.* 1995; Landlinger *et al.* 2012), but it seems plausible that even modest reductions in muscle



function with age might negatively affect performance in athletes working at the upper limits of their physical ability.

Serve accuracy also rose over age, peaked and then dropped, but in this case, accuracy peaked in slightly older players (late rather than mid-twenties). Accuracy relies on nervous and sensory systems and their integration with the motor system (Briffa and Lane 2017). There is some evidence that elements of the nervous and sensory systems do not show pronounced functional declines until relatively late in the aging process. For example, auditory, somatosensory and visually evoked potentials, which tell us how the brain responds to particular stimuli, are relatively constant in adults aged between 20 and 60, after which they begin to decline (Allison *et al.* 1983). Accuracy in simple motor tasks does not differ in participants under 35 and over 50, but older participants recruit additional cortical and subcortical areas to achieve accurate responses (Mattay *et al.* 2002). It seems that aging humans can maintain accuracy, or use alternative mechanisms to preserve accuracy, better than they can maintain power.

Given that on average, power and accuracy both showed declines over age, there does not seem to be much scope for trait compensation. However, when we looked at individuals rather than at the “population” level, there were clear signs of trait compensation. Players that showed severe declines in serve speed also showed pronounced increases in serve accuracy. These increases in accuracy may help buffer against overall deterioration in serve speed to preserve overall serve performance. Increases in accuracy that compensate for declines in power may explain why in hunter-gatherer societies, men gain greatest hunting success long after peaking in physical strength (Walker *et al.* 2002). A previous study found no obvious signs of trait compensation in athletes (Lailvaux *et al.* 2014). This difference may reflect that the potential for trait compensation for a given action will depend on the suite of traits required to complete that action.

While serve speed and accuracy differed across the sexes, we found no evidence of sex differences in patterns of change for either trait. Qualitatively, women tend to begin playing elite tennis earlier: our database contains 33 women who were playing at elite level aged 18, but only 11 men aged 18 or under. This makes sense because girls start puberty earlier than boys (Yousefi *et al.* 2013). An earlier analysis of tennis players found that generally, women’s performance (measured as the chances of winning) peaks earlier than men’s (Guillaume *et al.* 2011). Unlike Guillaume *et al.* (2011), we did not see sex differences in functional declines. This is surprising given that sex differences in athletic performance over age are widespread. Lailvaux *et al.* (2014) found sex differences are visible early in the aging process (mid-twenties) in basketball players. Baker and Tang (2010) analyzed athletes from a range of sports and found that the age at which age-specific record performance drops to 75% of the record performance at age 30 is typically younger in women than in men. If sex differences in athletic performance are widespread, why do we not see them in our analyses?

One possibility is that sex differences in functional senescence are the norm for these traits in the population as a whole, but we do not detect them because our data-set consists entirely of outliers.

Athletes represent the extreme upper end of any distribution for human physical ability and so data on athletes may be limited with respect to what it can tell us about the general population. This may be particularly true if elite players who train intensively to preserve their strength have developed techniques that mitigate and compensate for pronounced age-associated declines. Furthermore, any athlete that does experience severe senescence, may be less likely to feature in the data-set at all (or to remain in the data-set to advanced age) because they retire earlier.

Alternatively, had we studied the wider population perhaps we would not have seen sex differences in functional declines either, as these are by no means universal. Ultra-marathon runners for example show conserved trajectories of deteriorating performance across the sexes (Knechtle *et al.* 2012). It seems likely that we should only expect divergent patterns of decline across the sexes if 1) the strength of natural or sexual selection acting on these traits (or correlated characters) shows dissimilar patterns of change with age in either sex or 2) the proximate costs of expressing traits differs across the sexes. In this case, pronounced sex differences in functional senescence may be much more likely to manifest after the age of female menopause, when direct selection acting on women (but not men) drops precipitously. The genetic architecture of traits may also be important in shaping sex-specific patterns of functional decline. Because the sexes share a genome, strong selection on one trait (e.g. selection for male musculature), could generate a correlated response in the other sex, meaning that in principle, strong selection on the preservation of function in one sex over age, could promote preservation of function in the other sex.

We cannot say why we do not see sex differences in the traits we studied here as it seems likely that patterns of sex-specific functional senescence are influenced by the complex interplay between natural and sexual selection, the proximate constraints on expressing a trait, and the genetic architecture underlying that trait. We suggest that data on athletes, inevitably outliers of human ability, are not appropriate for dissecting these complex interactions.

#### **AUTHOR CONTRIBUTIONS**

CRA and UB conceived the study; CRA, UB, SB and DJH designed the study; SB and MDS collated data; AS performed the analyses; CRA wrote the manuscript; all authors edited the manuscript.

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#### **DATA ARCHIVING**

The data used in these analyses originate from on [www.OnCourt.info](http://www.OnCourt.info).

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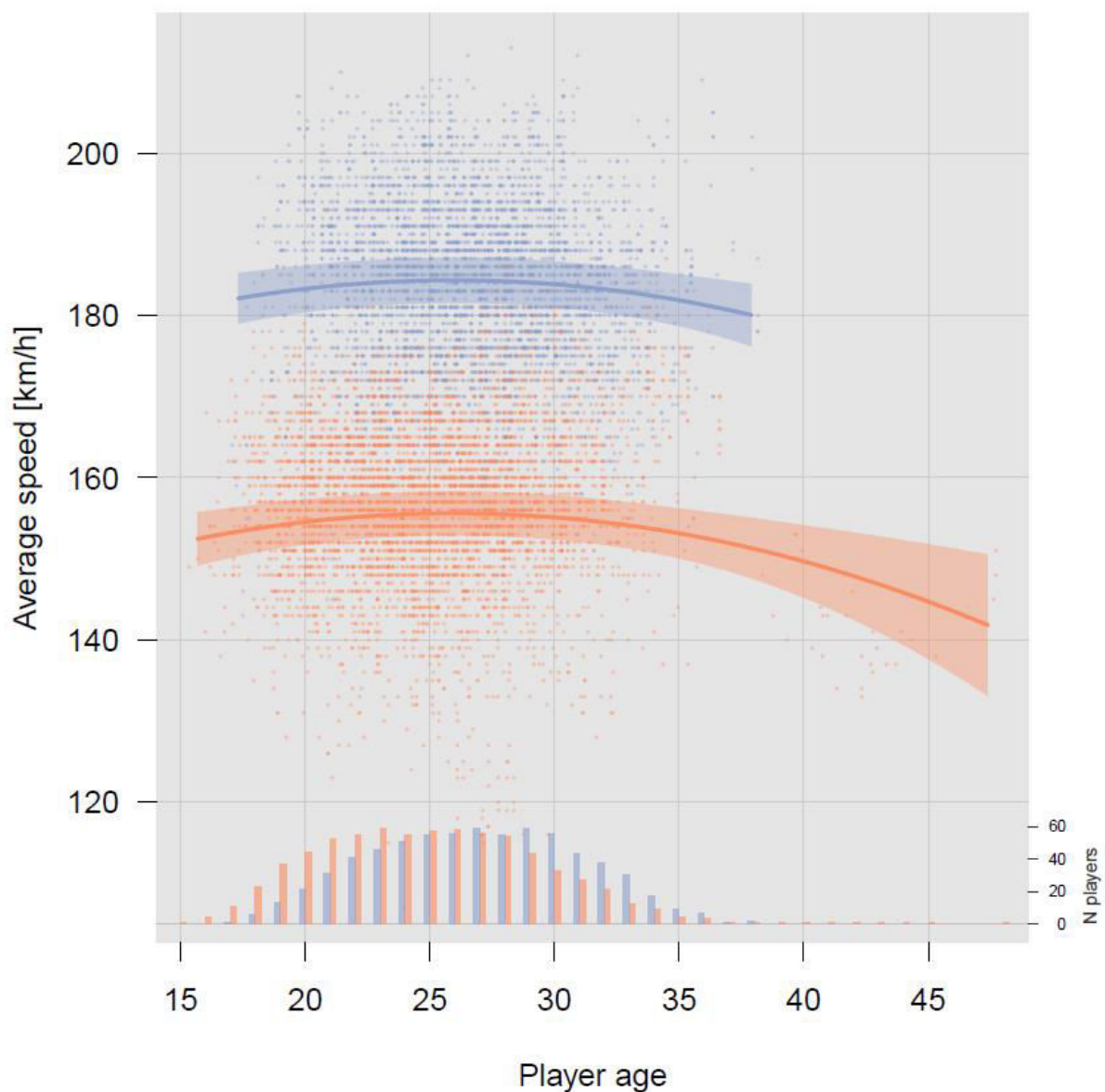
**TABLE 1.** Model summaries for linear mixed effects models on serve speed and serve accuracy.

Response variable	Fixed effects	Centred/ Scaled	Full model Estimate [SE]	LRT $\chi^2$	p	Minimal model Estimate [SE]
Serve speed [km/h] <i>mean (SD)=170 (16.7)</i>	Intercept		170.07 [1.22]	–	–	170.00 [1.22]
	Sex (male)	y/n	<b>29.73 [1.34]</b>	<b>222.51</b>	<b>&lt;0.001</b>	<b>29.50 [1.33]</b>
	Age linear	y/y	-0.31 [0.45]	0.57	0.451	
	Age quadratic		<b>-0.55 [0.14]</b>	<b>11.18</b>	<b>0.001</b>	<b>-0.48 [0.14]</b>
	Sex: Age linear		0.68 [0.50]	1.84	0.175	
	Sex: Age quadratic		-0.30 [0.25]	1.34	0.247	
	Sets	y/y	<b>-0.50 [0.08]</b>	<b>34.56</b>	<b>&lt;0.001</b>	<b>-0.50 [0.08]</b>
Serve accuracy [%] <i>mean (SD)=62 (7.9)</i>	Intercept		61.96 [0.74]	–	–	61.98 [0.80]
	Sex (male)	y/n	<b>-2.23 [0.76]</b>	<b>7.51</b>	<b>0.006</b>	<b>-1.99 [0.72]</b>
	Age linear	y/y	<b>0.57 [0.21]</b>	<b>7.14</b>	<b>0.008</b>	<b>0.59 [0.21]</b>
	Age quadratic		<b>-0.51 [0.12]</b>	<b>17.20</b>	<b>&lt;0.001</b>	<b>-0.51 [0.12]</b>
	Sex: Age linear		0.08 [0.37]	0.19	0.665	
	Sex: Age quadratic		0.22 [0.23]	0.87	0.351	
	Sets	y/y	<b>0.23 [0.10]</b>	<b>5.17</b>	<b>0.023</b>	<b>0.23 [0.10]</b>

*Full model formulae: lmer(response~1+sex+age+agequad+sex:age+sex:agequad+sets+(1+age+agequad|player\_ID)+(1|tournament)+(1|year))*

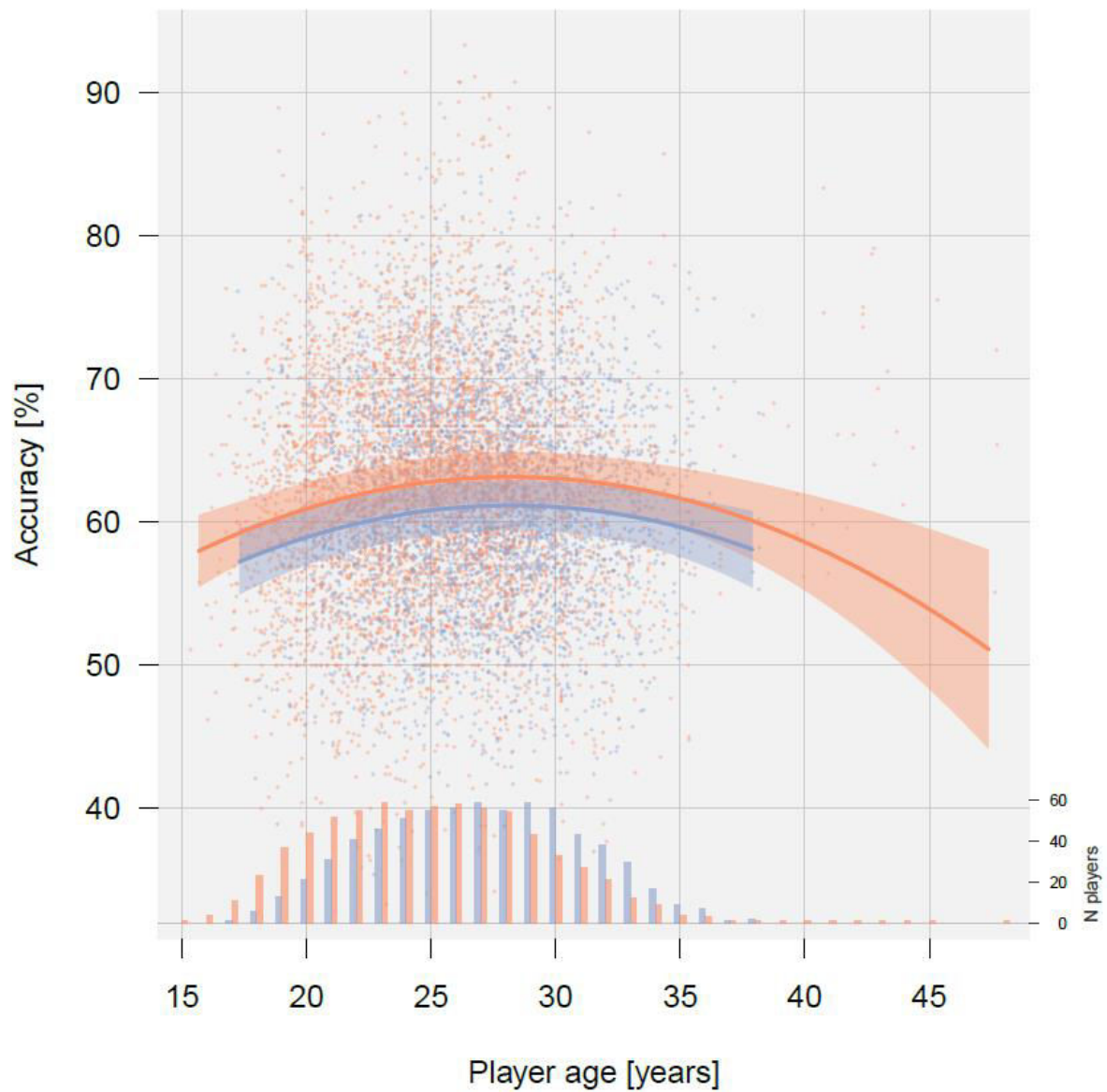
Full models included sex, age (as both a linear and a quadratic term), two-way interactions between sex and age, and number of sets played as fixed effects. Age and number of sets were scaled and centered, and sex was centered, so that the global intercept corresponds to the prediction for a hypothetical match over 2.9 sets played by a player with no sex and of average age (25.94 years old). Age and sets effects correspond to an increase in 1SD of age (3.95 years) and number of sets (0.9 sets). Random intercepts as well as random linear and quadratic slopes over age were fitted for individual players, as were random intercepts for tournament and year (see main text and Table S1). Fixed effects estimates and standard errors from full models are shown in comparison to coefficients from minimal models. Minimal models were obtained through stepwise model selection, based on likelihood ratio tests and starting with the removal of interaction terms (see main text).

**FIGURE 1.** Changes in average first serve speed (km/h) over age in women (red) and men (blue). Lines and shaded areas represent model predictions and approximate 95% confidence intervals from a linear mixed model including sex and a quadratic effect of age as fixed effects, and athlete identity, year and tournament as random intercepts as well as random linear and quadratic athlete-specific slopes (see main text). Coloured bars at the bottom show the number of female and male athletes with available data for a given age category.

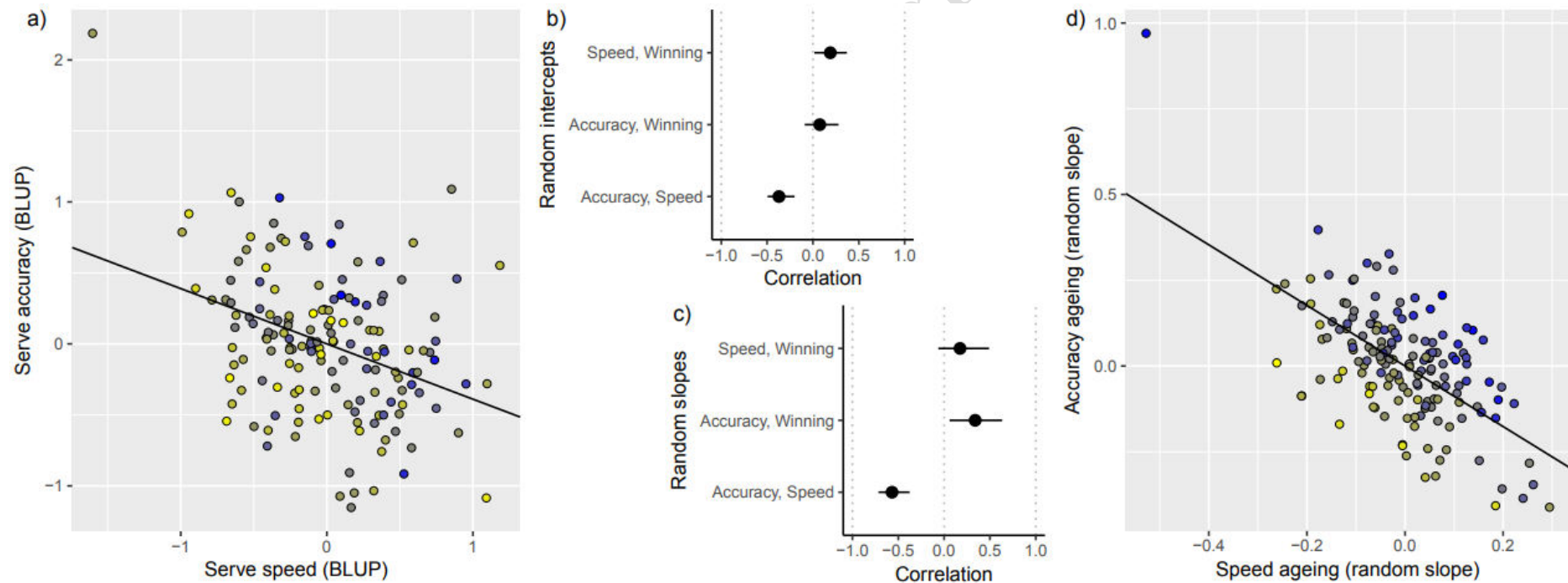




**FIGURE 2.** Changes in serve accuracy (proportion of first serves delivered) over age in women (red) and men (blue). Lines and shaded areas represent model predictions and approximate 95% confidence intervals from a linear mixed model including sex and both a linear and a quadratic effect of age as fixed effects, and athlete identity, year and tournament as random intercepts as well as random linear and quadratic athlete-specific slopes (see main text). Colored bars at the bottom show the number of female and male athletes with available data for a given age category.



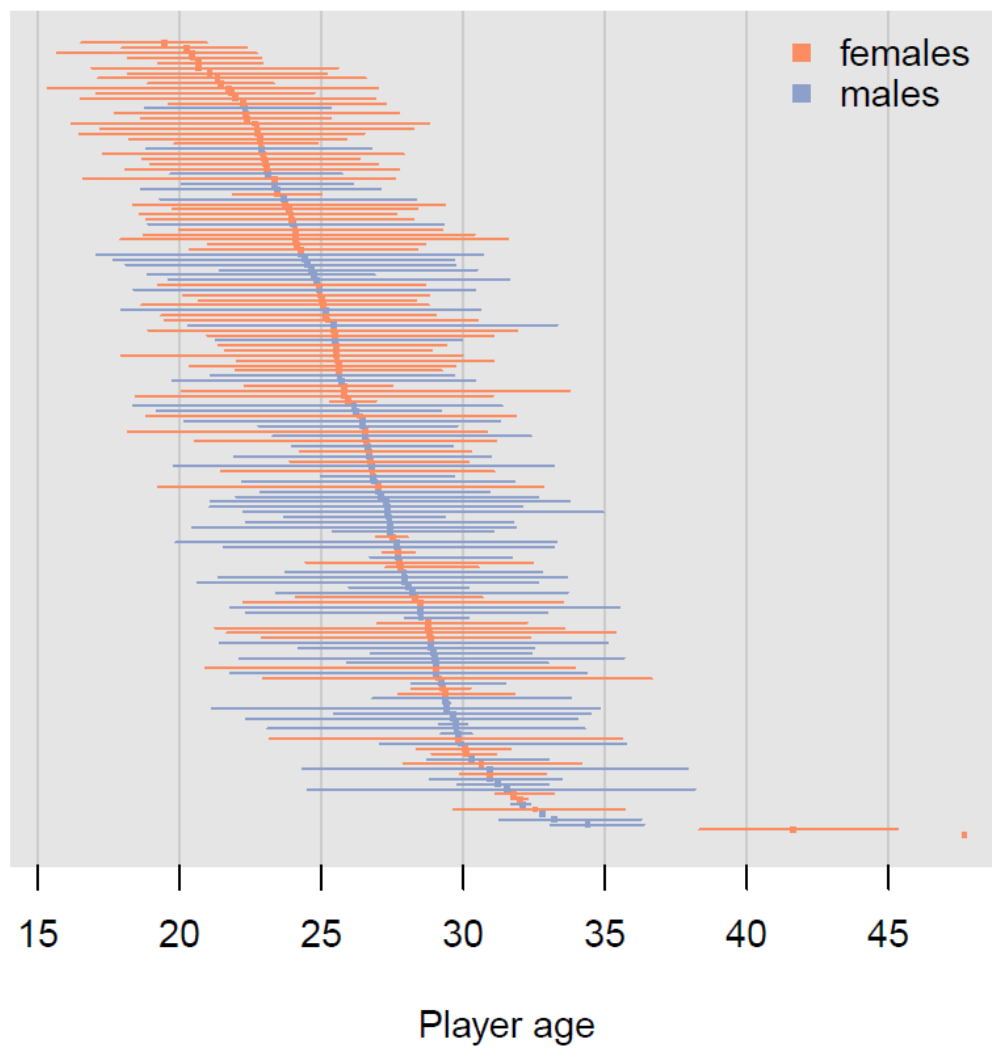
**FIGURE 3.** Illustration of trait compensation: a) negative correlation between speed and accuracy at the individual athlete level (random intercepts); d) negative correlation in individual aging trajectories between serve speed and serve accuracy (random slopes). Best linear unbiased predictors (BLUP) and random slopes for individual players were obtained from a tri-variate *mcmcGLMM* (Hadfield 2010), including serve speed, serve accuracy and winning with fixed and random effects as specified in the main text. Colour gradients of points in the large panels indicate between-athlete variation in a) winning and in b) the age trajectory of winning, with darker shading (online version: blue) indicating larger values. Panels b) and c) show estimates and credible intervals for pairwise correlations, calculated from the posterior distribution of among-individual between-trait covariance's by dividing the covariance of two focal traits by the product of the square root of their variances (following Houslay and Wilson (2017)). Note that correlations between serve traits and winning were all positive but two of four credible intervals overlapped zero (panels b and c).



## Electronic supplementary material

### Do elite tennis players show sex-specific senescent declines?

**Figure S1:** Overview of careers of male and female elite tennis players covered in our dataset. Points and lines represent mean age and age range for all Grand Slam matches played by top-tier individual female (orange) and male (blue) athletes between 2003 and 2017, and are ordered by increasing average age.



## Supplementary methods

### *Multivariate modelling in MCMCglmm*

We explored among-individual between-trait covariance between serve speed and accuracy, and winning using in a tri-variate *MCMCglmm* (Hadfield, 2010). Here, in addition to predictor variables, the response variables serve speed and serve accuracy were scaled to standard deviation units prior to analysis, enabling more meaningful comparison of effect sizes across these traits and assisting multivariate model fitting. For our fixed effects, the random effects associated with player identity (random intercepts and slopes) and the residuals, we fitted an unstructured variance-covariance matrix that allows estimation of covariances between parts of the model. We fitted variances but no covariances for the random effects *tournament* and *year* on serve speed and accuracy. Winning was assumed (and observed) to have no substantial variance across tournaments and years, as the number of matches available to be won will be roughly constant. We observed that variance and covariance components involving random quadratic slopes were very small and showed substantial autocorrelation even with extensive thinning. To improve chain mixing, we thus removed random quadratic slopes from our model. We fixed the residual variance for winning (binary outcome) at 10.

The final model was run for 220,000 iterations with a thinning interval of 100 and a burn-in of 20,000 with parameter expanded priors. This resulted in 2000 samples from the posterior for which autocorrelation between successive samples for parameters was less than 0.1. The results reported here were obtained using parameter-inflated priors. However, we additionally checked that our results were robust to variation in priors and that multiple runs converged on the same posterior distribution using Gelman-Rubin diagnostics. The mean and credible intervals for among-match and among-individual correlations between traits were estimated from our *MCMCglmm* model (co)variances. Correlations were interpreted as significant when the 95% credible intervals did not overlap zero. For visual illustration of those correlations, we extracted best linear unbiased predictors (BLUPs) and random slope estimates from our fitted models (Houslay & Wilson, 2017).

### *Supplementary references:*

Hadfield, J.D. 2010. MCMC Methods for Multi-Response Generalized Linear Mixed Models: The MCMCglmm R Package. *J. Stat. Softw.* **33**: 1–22.

Houslay, T.M. & Wilson, A.J. 2017. Avoiding the misuse of BLUP in behavioural ecology. *Behav. Ecol.* **28**: 948–952.

**Table S1:** Comparison of fixed and random effects estimates from a tri-variate *MCMCglmm* model and univariate *lme4* models on serve speed, serve accuracy and winning. Normally distributed response variables and player age were scaled to zero mean and 1SD. Females and males were assigned a value of -0.5 and 0.5, respectively, so that the intercept is calculated for a hypothetical game over 2.9 sets played by a player with no sex and an age of 25.94 years.

Response Model	Serve speed (centred & scaled)				Serve accuracy (centred & scaled)				Winning			
	<i>MCMCglmm</i>		<i>lmer</i>		<i>MCMCglmm</i>		<i>lmer</i>		<i>MCMCglmm</i>		<i>glmer</i>	
Fixed effects	Est.	95% CI	Est.	StdE	Est.	95% CI	Est.	StdE	Est. <sup>†</sup>	95% CI <sup>†</sup>	Est.	StdE
(Intercept)	-0.003	[-0.18,0.19]	-0.004	0.07	0.005	[-0.26,0.28]	0.001	0.10	0.49	[0.35,0.63]	0.47	0.06
sexM	1.76	[1.60,1.92]	1.77	0.08	-0.29	[-0.46,-0.10]	-0.25	0.09	0.36	[0.10,0.63]	0.31	0.13
Age	-	-	-	-	0.07	[0.02,0.13]	0.08	0.03	0.13	[0.03,0.22]	0.12	0.05
Age^2	-0.03	[-0.04,-0.02]	-0.03	0.008	-0.06	[-0.09,-0.04]	-0.06	0.02	-0.34	[-0.29,-0.18]	-0.22	0.03
Sets played	-0.03	[-0.04,-0.02]	-0.03	0.005	0.03	[0.003,0.05]	0.03	0.01	-0.27	[-0.34,-0.20]	-0.25	0.03
Random effects	Var	95% CI	Var	SD	Var	95% CI	Var	SD	Var <sup>†</sup>	95% CI <sup>†</sup>	Var	SD
Player	0.24	[0.19,0.31]	0.23	0.48	0.27	[0.23,0.38]	0.30	0.55	0.49	[0.38,0.67]	0.44	0.66
Age (slope)	0.02	[0.01,0.03]	0.02	0.14	0.05	[0.03,0.07]	0.04	0.20	0.11	[0.07,0.22]	0.12	0.34
Age (slope^2)	-	-	0.003	0.05	-	-	0.01	0.10	-	-	-	-
tournament	0.02	[0.001,0.07]	0.03	0.17	0.02	[0.005,0.23]	0.006	0.08	-	-	-	-
Year	0.02	[0.01,0.06]	0.008	0.09	0.007	[0.002,0.2]	0.03	0.17	-	-	-	-
Residual	0.105	[0.102,0.108]	0.10	0.32	0.66	[0.64,0.68]	0.66	0.81	-	-	-	-

<sup>†</sup> Because the residual variance was fixed at 10 for the binomial part (winning) of the tri-variate *MCMCglmm* model, parameters were rescaled following Jarrod Hadfield's course notes (page 51; <https://cran.r-project.org/web/packages/MCMCglmm/vignettes/CourseNotes.pdf>):

For fixed effects  $Est./\sqrt{1 + c2 * 10}$  and for random effect variances  $Var/(1 + c2 * 10)$ , where  $c2 = ((16 * \sqrt{3})/(15 * \pi))^2$