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TRAIT COMPENSATION AND SEX-SPECIFIC AGING OF PERFORMANCE IN MALE AND FEMALE PROFESSIONAL BASKETBALL PLAYERS

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Phenotypic traits are often influenced by dynamic resource allocation trade-offs which, when occurring over the course of individual lifespan, may manifest as trait aging. Although aging is studied for a variety of traits that are closely tied to reproduction or reproductive effort, the aging of multiple traits related to fitness in other ways are less well understood. We took advantage of almost 30 years of data on human whole-organism performance in the National Basketball Association (USA) to examine trends of aging in performance traits associated with scoring. Given that patterns of aging differ between sexes in other animal species, we also analyzed a smaller dataset on players in the Women's National Basketball Association to test for potential sex differences in the aging of comparable traits. We tested the hypothesis that age-related changes in a specific aspect of overall performance can be compensated for by elevated expression of another, related aspect. Our analyses suggest that the aging of performance traits used in basketball is generally characterized by senescence in males, whereas age-related changes in basketball performance are less evident in females. Our data also indicate a different rate of senescence of different performance traits associated with scoring over a male's lifetime.

KEY WORDS: Compensation, life history, sex differences, trade-offs, whole-organism performance.

Aging in most animals is a consequence of weak selection pressure on genes expressed later in life. For traits that are not closely tied to reproduction, this tends to manifest as trait senescence as an individual ages, particularly for traits that are important in early-life stages as opposed to late adulthood. By contrast, those traits that are closely related to reproduction are expected to be expressed more strongly due to terminal investment as survival prospects decline (Hunt et al. 2004; Zajitschek et al. 2012). However, age-specific energetic investment via resource allocation can be affected by the nature and scheduling of reproductive effort (Bonduriansky et al. 2008), and allocation priorities consequently can and do differ between males and females, potentially resulting in sex-specific patterns of aging for certain traits, but not for others (Nussey et al. 2009). Life histories are therefore shaped by overall selection to represent a balance between somatic maintenance and reproductive investment (Stearns 1989; Roff 1992), and this tension between natural and sexual selection pressures on trait aging can lead to a variety of age-related trajectories that may differ between males and females of a given species (Bonduriansky et al. 2008; Maklakov et al. 2009). This is especially true for traits that affect both reproduction and survival (Lailvaux et al. 2011). Although the reproductive factors affecting sex-specific trait aging are receiving increasing attention (Maklakov 2008; De Loof 2011; Massot et al. 2011; Zajitschek et al. 2012), understanding the influence of selection pressures on sex-specific aging in nonreproductive contexts (and, indeed, on the existence and maintenance of sex-differences in those contexts; Cullum 1998; Lailvaux 2007) is an ongoing challenge (Zajitschek et al. 2009a,b).

Age-related changes in a specific phenotypic trait may also be affected by the expression of others. For instance, traits such as whole-organism performance (broadly defined as any measure of an organism conducting a dynamic, ecologically relevant task, e.g., jumping, running, or biting; see Bennett and Huey 1990; Irschick and Garland 2001; Lailvaux and Irschick 2006) are embedded within a complex phenotype involving numerous reticulate genetic and phenotypic correlations (Ghalambor et al. 2003). Changes in expression of a given trait may consequently modify or modulate that of related traits, especially those at relatively lower levels of biological organization (Swallow et al. 2009). Furthermore, the principle of allocation posits that excellence in one task is typically attained at the cost of average performance in others (Gadgil and Bossert 1970). For whole-organism performance traits such as locomotion, this constraint tends to be driven by trade-offs among trait expression caused by conflicting demands on the muscular-skeletal system. For example, selection on burst locomotor capacity can trade-off with endurance capacity in some species of lizards (Vanhooydonck et al. 2001) and frogs (Herrel and Bonneaud 2012), such that maximizing both burst and endurance capacities in the same individual is not possible. Consequently, if trait performance within the context of a given ecological task drops-off or senesces, this may create an opportunity for that trait's fitness contribution to be compensated for by elevating the expression of a different trait to meet the necessary fitness benchmark. Although compensation is an important emerging theme under evolutionary scenarios such as sexual selection and intralocus sexual conflict (e.g., Husak et al. 2011), thus far, this notion of dynamic compensation that might occur over individual lifetimes among groups of related traits has received little attention within the evolutionary literature on aging.

Age-related compensatory trade-offs in performance have previously been considered primarily within the context of development and ontogeny. For example, poor early nutrition can have pervasive long-term effects on the adult phenotype, and consequently compensation for early developmental energy deficits can occur at subsequent life stages (Royle et al. 2006). Such examples of performance compensation over ontogeny, however, are usually intertwined with compensatory juvenile growth that seldom persists into adulthood. In many cases, this may be due to inherent constraints on compensation, which may for example need to occur prior to termination of cell proliferation and differentiation. Far less understood are dynamic compensatory allocations that may occur during the adult phase (i.e., following ontogeny) (but see Auer 2010, who showed that compensation for juvenile conditions can occur in adult guppies, *Poecilia reticulata*). If such dynamic compensation is common, then it could potentially influence aging in the expression and performance of key ecological tasks by alleviating the costs of senescence in a particular trait driving that task. Given the differences in age trajectories between males and females in many species, such compensation may be constrained in, or alternatively only required by, one or the other sex. An ideal system for studying trait compensation during aging would therefore be one in which the contributions to an important fitness task could be separated into its component categories and tracked over individual lifetimes in both males and females within a similar context or environment.

In this study, we consider aging in a suite of performance traits exhibited by professional basketball players in the United States' National Basketball Association (NBA) and Women's National Basketball Association (WNBA) over the last 30 years. Both the NBA and the WNBA comprise a large number of players, many of whom play at the highest professional level for a significant part of their adult lives. Furthermore, studies of aging in humans have noted that athletes are a "model population" for studying both performance and aging given that they train intensively over all or most of their lifetimes and generally show very little change in body mass or composition over that time (Hill 1925; Moore 1975). However, while studies of aging in human athletes have been valuable for understanding age-related changes in specific performance traits, little is known about how multiple performance traits may trade-off over individual lifetimes. Van Damme et al. (2002) analyzed human athletic data to show that trade-offs exist between burst power and exertion in elite decathletes for whom both types of performance are important. A large literature on human performance has shown that different athletic traits show different rates of aging; for example, Baker and Tang (2010) examined human aging in a variety of different athletic disciplines ranging from swimming to weightlifting and found that while all traits ultimately senesced over a long enough time scale, weightlifting exhibited the fastest and greatest decline with age, and that jumping and weightlifting declined the most in women relative to men. Indeed, the differing costs of reproduction in males and females, coupled with sex differences in body composition and the general metabolic costs of performance maintenance, might lead one to predict that males and females would exhibit different age trajectories with regard to whole-organism performance traits, although the nature of such differences might also be expected to differ among performance traits.

Given these nonuniform changes in aging of different types of athletic performance, age-related compensation in an overall performance trait, such as total number of points scored by an individual per basketball game, might be possible. Scoring is a particularly relevant metric for several reasons. First, all players are required to score for a team to be successful. Second, scoring captures a range of performance traits, and is therefore a useful proxy of general whole-organism performance. Any age-related changes in whole-organism performance will therefore be reflected as a change in scoring ability. Third, achieving different score types successfully is a result of integrating multiple whole-organism performance traits/abilities (e.g., burst speed, strength, motor, and visual accuracy) that may interact in different ways for each of the multiple ways of scoring in basketball. Two-point field goals, for example, can be scored from any area on the court within the three-point line, and may require different skills when in the key—the area under the basket that is bounded by the free-throw lanes—compared to when outside of it (i.e., greater strength vs. greater agility, respectively), and are usually performed under heavy competitive influence. By contrast, three-point field goals can only be scored over a relatively longer distance from outside the three-point line, which consequently may require more power and, especially, greater accuracy, and thus have a higher probability of failure than two-pointers. Finally, free throws are always taken from the same position, with no competitive influence and a low probability of failure, but require individuals to successfully ignore both player and non-player distractions while integrating accuracy and power. Scoring therefore satisfies the condition of a physiological performance metric that can be separated into different components, each with its own unique set of challenges. Any of these components might compensate for another over time if, for example, player abilities change as they age. This attribute is particularly important when considering sex-differences, as different sex-specific ageing trajectories for specific traits could conceivably result in different patterns of trait compensation, or even the absence thereof altogether, in one sex relative to the other. Scoring is also arguably the best metric of player ability, as composite measurements of player performance (both individually and relatively) are strongly swayed by scoring ability compared to other metrics (e.g., steals, blocks, rebounds) (see Hollinger 2005 for a detailed discussion).

We used a large, freely available database on professional basketball players from both the National Basketball Association (NBA) and the Women's National Basketball Association (WNBA) to test the two following hypotheses regarding the aging of basketball performance (using points scored as a proxy for overall basketball performance):

(1) Men and women show different patterns of aging in overall basketball performance.
(2) Men and women show different patterns of compensation for aging in basketball performance, as indicated by distinct patterns of aging for different score types (i.e., two-point field goals vs. three-point field goals vs. free throws).

Methods

We collected data on individual performances in the NBA and the WNBA from http://www.bballsports.com and http://www.basketball-reference.com. Supplementary data regarding ages and heights of individual players were sourced from player biographies or from online images of trading cards as required. For each individual and for each year played by that individual, we collected data on player age, height, total points scored, total points from two-point field goals, total points from three-point field goals, total points from free-throws, and total playing time. Only players with complete records for each of these key variables were included in the final analyses. We did not analyze variation in position for two reasons; first, positions in basketball are extremely fluid relative to other team sports such as football or rugby, and players may therefore take on multiple functional roles during the course of a game regardless of their primary designated position. More importantly, preliminary analyses showed that variation in height is very closely associated with variation in position; therefore, to avoid statistical issues regarding collinearity and variable redundancy, we did not include position as a covariate in the final analyses. Ultimately, we were able to obtain full data for 1035 NBA players over the period from 1979–2010 (as the three-point shot debuts in 1979), and for 540 WNBA players over the period from 1998–2009. Because all individuals do not necessarily play every game in a season, nor do they even always play for entire duration of games, we corrected for play time by analyzing points scored per minute both for overall points scored and for each point category (two-point field goals, three-point field goals, and free-throws).

STATISTICAL ANALYSES

We compared heights of males and females in our dataset using a *t*-test. To explain the variation in number of points scored over professional playing careers, we fitted a series of linear mixed-effects models using the lme function of the nlme package version 3.1–109 (Pinheiro et al. 2013) for R analytical software version 3.0.1 (R development core team 2013). All models included a random intercept for each individual, as well as age as a random slope (Schielzeth and Forstmeier 2009). For total number of points/min, we fitted a global model with sex and age as fixed effects. To analyze the points scored by point type (i.e., two-pointers, three-pointers, and free throws), we fitted a global model with $(\text{points/min})^3$ [determined by Box–Cox transformation using the MASS package in R] as a function of sex, age, and point type with the number of shots of each type attempted as a covariate. Separate models were then fit for men and women to explain intrasexual variation for each points model (i.e., total points and point type). Variables were transformed to meet assumptions of normality and homoscedasticity as required.

For all models, both linear and quadratic terms, as well as all possible interactions between them, were initially fitted for all factors. Subsequent model simplification and selection was based on deletion tests using log-likelihood ratios, which enabled us to find the "minimum adequate model" to describe the data (Crawley 1993). Models with and without random effects were similarly compared using maximum likelihood. Following model reduction, the minimum adequate model for each analysis type was refit using REML. To visualize the curvilinear age effects and the categorical effects of sex and point type on points scored, we plotted smoothed curves drawn from best-fitting generalized additive models (GAMs) using the mgcv package for R (Wood 2011).

TEAM QUALITY

To control for the effects of team quality on aging of points scored, we conducted a separate set of analyses identical to those described above, except this time including an index of team quality for each season played by each individual. This index was calculated as the percentage of games won by the team in a given season. In cases where players were traded during a season, and consequently played for multiple teams, we calculated this index as the average of the team quality from the years before and after the trade, respectively. However, in 450 cases players were traded multiple times in consecutive years; team quality therefore could not be calculated, and these data rows were removed from the dataset. Because the lengths of the datasets with and without the team quality index are consequently different, we clearly differentiate between these two analyses here.

Results

TOTAL POINTS

Height differed significantly between the sexes, with males being taller than females (200.82 ± 0.29 cm, 183.26 ± 0.40 cm, respectively; $t_{1,\,1573} = 35.68$, $P < 0.001$). The model that best described variation in total number of points scored/min contained linear, quadratic, and cross-product terms (Table 1). The interactions between sex and both the linear and quadratic age terms indicate divergent age trajectories for males and females. Indeed, males and females exhibit strikingly different patterns of aging, with a male peak evident at approximately 25 years of age, and followed thereafter by a marked decline (Fig. 1A). The points/min aging curve for females, by contrast, exhibits no such equivalent peak (Fig. 1B). The 95% confidence intervals (CI) for this female curve are also noticeably wider than the corresponding male curve, particularly for intermediate ages, likely as a result of the overall smaller sample size and shorter timespan for WNBA relative to NBA players in our dataset. The fan-shaped CI's at either

Table 1. Best-fitting model describing the variation in the (total number of points scored/min)$^{1/2}$ over individual playing careers by sex and age (in years), controlling for height (in cm). The baseline category for sex is female. Thus, the reported values give estimated change in points/min)$^{1/2}$ between the category named in the table and the baseline category.

Model term	Coefficient	SE
Intercept	0.035	0.39
Sex	0.74	0.39
Age	0.04	0.027
Age^2	-7.5×10^{-4}	4.9×10^{-4}
Height	-4.2×10^{-4}	4.9×10^{-4}
Sex:Age	−0.049	0.028
Sex:Age^2	8.6×10^{-4}	5.1×10^{-4}

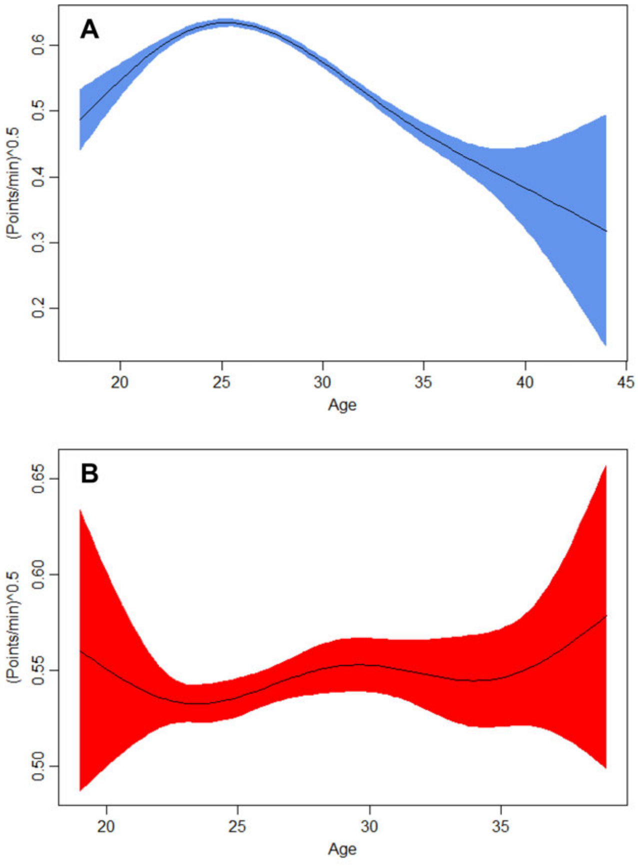

Figure 1. Relationships between total points scored and age for professional male (A) and female (B) basketball players. Shaded areas are 95% confidence intervals. Note the smaller age range for females relative to males.

end of the age scale for both sexes reflect the relative paucity of professional basketball players in their very early twenties and late thirties/forties, particularly for women. Indeed, no women have been recorded as playing into their forties in our dataset (age mean ± SE years, min–max; Men: 27.04 ± 0.07, 18–44; Women: 26.01 ± 0.147, 19–39), as opposed to a handful of men who have done so, up to a maximum age of 44.

POINT TYPE

When analyzing points scored by score type, sex, and age, the best fitting model retained a significant three-way interaction between score type, sex, and the quadratic aging term (Table 2). Thus, different score types exhibit different nonlinear aging patterns between the sexes. Indeed, while the point type models for males and females both retained similar type-by-age quadratic interactions (Table 3), the shapes of those curves differ between males and females (Fig. 2). Within males, the aging curve for points/min from three-point field goals was distinct from those curves for two point field goals and free throws, with a peak occurring at approximately age 30 for three-point field goals versus approximately 25 for both of the other two score types (Table 3A). For women, the three-point field goal curve is also distinct from that of the other two points types (Table 3B), with an arguably flatter and earlier peak than for males (~25 as opposed to 30) (Fig. 2B).

TEAM QUALITY

Team quality overall had little effect on the aging models, despite the slightly smaller size of the quality-controlled dataset (see Supplementary Results, Supporting Information Tables S1–S3). The only quality-controlled model that differed from the model without the quality term was that for male point type, which lacked the linear Type:Age interaction (Supporting Information Table S3). This does not change the qualitative nature of our results, as the male point type curves are all clearly nonlinear (Figs. 1A, 2A).

Discussion

Aging is a plastic life-history trait, and as such is influenced by a variety of factors including diet (Maklakov et al. 2009; Zajitschek et al. 2012), social environment (Kasumovic et al. 2011), mating history (Lailvaux et al. 2011), and many others. By taking advantage of a unique, long-term dataset, and analyzing indicators of basketball play, we show that the aging of scoring ability (which reflects aging in the underlying whole-organism performance traits that are tied to scoring) differs between males and females. Furthermore, these data show that within both sexes there is a clear difference in the aging of two important performance indicators (two-point vs. three point field goals), suggesting possible compensation in total points scored through relative adjustment of score type with age. This is also independent of the number of attempts made as individual's age, since "attempts" did not explain any variance in scoring success of any type and was therefore dropped from the best-fit model. This differential aging in males and females might be driven by intrinsic sex-differences associated with the physiological performance traits affecting basketball performance, or by differences in the environmental factors associated with male and female performance (see Lailvaux et al. 2011 for an example involving nonhuman whole-organism performance). Alternatively, sex-specific trade-offs in resource allocation involving whole-organism performance and other key fitness-related traits such as fecundity could also produce the observed male and female basketball aging curves independent of external environmental factors.

TOTAL POINTS

Our first hypothesis (i.e., that men and women show different patterns of aging for overall basketball performance) is supported by our best fitting model for total points/min that retains an interaction between sex and the quadratic aging term (Table 1), and indeed, the aging curves for total points/min clearly differ between men and women (Fig. 1). In particular, men exhibit a marked peak in points/min at approximately 25 years of age (Fig. 1A). This result is generally consistent with previous studies of human athletic performance, which show that peak age for a variety of different sports typically occurs in an individual's 20s (Schultz and Curnow 1988). In contrast to the result for men, however, the female aging curve for points/min is relatively flat and does not show any discernible peak (Fig. 1B), especially considering the wider confidence intervals for women compared with those for men. Thus, while total points/min peaks early in a player's career and subsequently declines, this value remains more or less constant for women over their entire careers (although we again emphasize the truncated nature of the WNBA dataset relative to that of the NBA as a result of the more recent creation of the WNBA). Sex-specific aging could be rooted in physiology, such as sex differences in metabolic rate or androgen levels, both of which are higher in men than in women (Wells and Plowman 1983; Mooradian et al. 1987). Indeed, both metabolic rate (Piers et al. 1998) and testosterone levels (O'Connell et al. 2011) decline with age, although whether metabolic rate aging is sex-specific is unclear. Furthermore, testosterone levels show only very gradual change in men (O'Connell et al. 2011), and are unlikely to account for the marked and relatively early decline in male scoring performance observed in this dataset. Nonetheless, physiological differences are a potentially important source of sex-specific variation in any performance dataset (Lailvaux 2007).

In addition to intrinsic physiological differences between men and women that might influence differential aging rates, a further likely explanation for the sex difference in performance

Table 2. Best-fit model results for (points/min)$^{0.3}$ scored as a function of sex, age, and point type (two pointers, three pointers, and free throws) over individual playing careers broken down by point type, in combination with sex and age (in years), and controlling for height (in cm). The baseline category for type is FT (free throws), and the baseline category for sex is female. Thus, the reported values give estimated change in (points/min)$^{0.3}$ between the category named in the table and the baseline category.

Model term	Coefficient	SE
Intercept	0.62	0.2
Sex (Male)	−1.277	0.21
Type (Three)	−0.9	0.21
Type (Two)	−0.05	0.21
Age	0.017	0.014
Age^2	-3×10^{-4}	2.5×10^{-4}
Height	−0.002	2.6×10^{-4}
Sex (Male):Type (Three)	0.47	0.219
Sex (Male):Type (Two)	0.087	0.219
Sex (Male):Age	0.106	0.015
Sex (Male):Age^2	−0.002	2.6×10^{-4}
Type (Three):Age	0.05	0.015
Type (Two):Age	0.008	0.015
Type (Three):Age^2	-8×10^{-4}	2.6×10^{-4}
Type (Two):Age^2	-1.1×10^{-4}	2.6×10^{-4}
Sex (Male):Type (Three):Age	−0.044	0.016
Sex (Male):Type (Two):Age	−0.004	0.016
Sex (Male):Type (Three):Age^2	8×10^{-4}	2.8×10^{-4}
Sex (Male):Type ((Two):Age^2	2.95×10^{-5}	2.8×10^{-4}

aging may lie in the different frequencies of games in the NBA versus the WNBA. An NBA regular season comprises 82 games (excluding additional playoff games) whereas a WNBA regular season is only 34 games. The NBA season is therefore considerably more physically demanding for the average full-season male player than for female players, and especially so for a team's "star" players who might be allocated more play time per game. Even if males and females experienced equivalent training and practice sessions, the roughly 140% average extra play time for men relative to women, year after year, is likely to be an important factor affecting the aging of basketball-related performance traits over a player's entire career. Thus, the more grueling schedule for the professional male versus female professional basketball players might account for the significant decline in points scored past the ages of 25 for males. Unfortunately, the NBA has not grown significantly in the number of teams from our first year of data in 1979 (only eight teams were added in a short period of time during our period of analysis) such that we cannot separate potential sex effects on performance aging from those of match frequency in our current data set. Furthermore, this result is difficult to evaluate

Table 3. Best-fit model results for (points/min)$^{0.3}$ scored as a function of both age and point type for (a) males and (b) females. The baseline category for type is FT (free throws). Thus, the reported values give estimated change in (points/min)$^{0.3}$ between the category named in the table and the baseline category.

(a) *Males*			(b) *Females*		
Model term	Coefficient	SE	Model term	Coefficient	SE
Intercept	−0.673	0.084	Intercept	0.796	0.19
Type (Three)	−0.411	0.065	Type (Three)	−0.897	0.218
Type (Two)	0.04	0.065	Type (Two)	−0.047	0.218
Age	0.125	0.004	Age	-1.1×10^{-4}	0.012
Age^2	−0.002	6.9×10^{-5}	Age^2	-5.5×10^{-6}	2.2×10^{-4}
Height	−0.002	3.2×10^{-4}	Height	−0.002	4.3×10^{-4}
Type (Three):Age	0.006	0.005	Type (Three):Age	0.05	0.016
Type (Two):Age	0.004	0.005	Type (Two):Age	0.008	0.016
Type (Three):Age^2	1.82×10^{-5}	8.1×10^{-5}	Type (Three):Age^2	-8.6×10^{-4}	2.8×10^{-4}
Type (Two):Age^2	-8.6×10^{-5}	8.1×10^{-5}	Type (Two):Age^2	-1.2×10^{-4}	2.8×10^{-4}

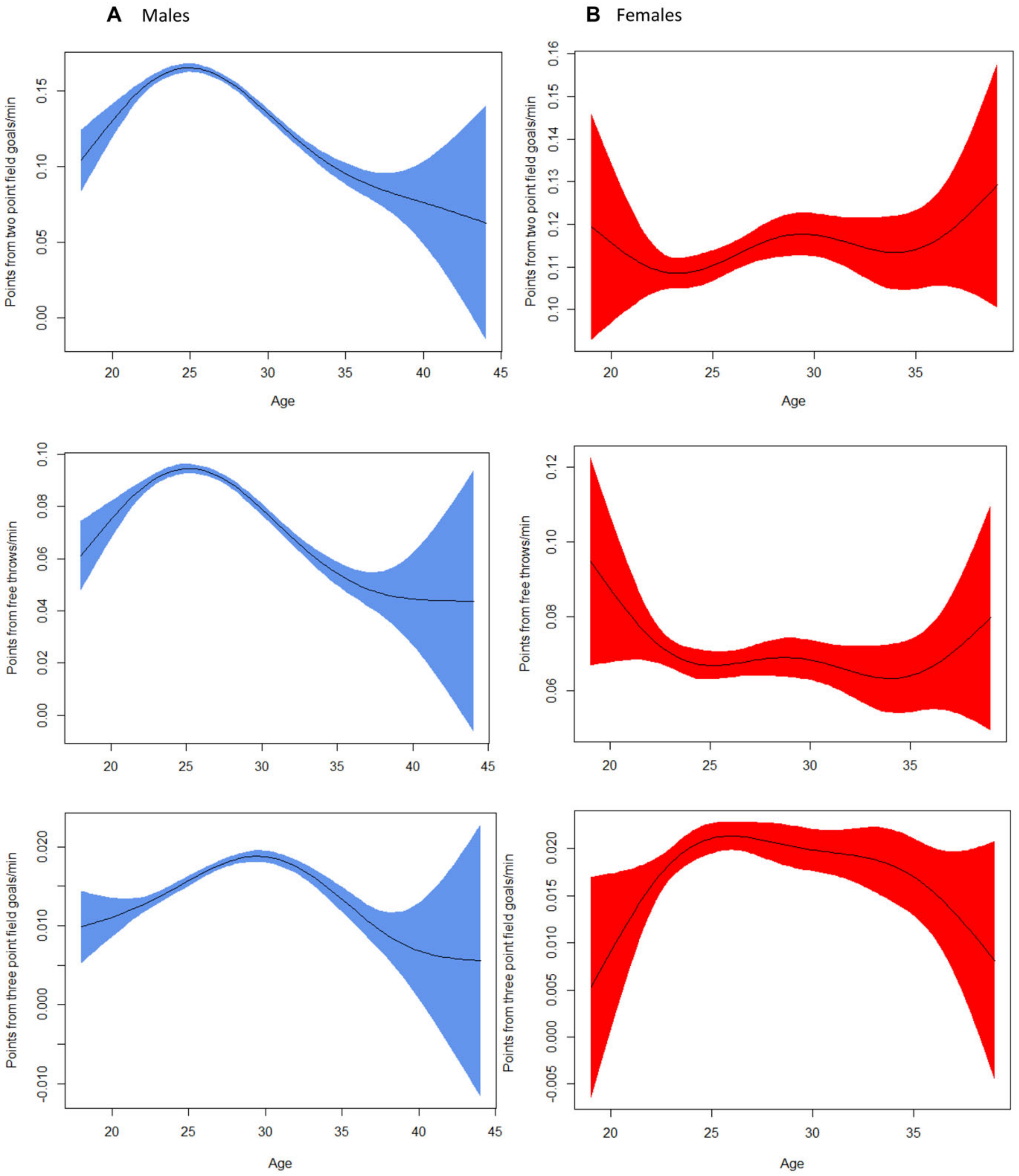

Figure 2. Relationships between age and points scored broken down by sex and point type. Shaded areas are 95% confidence intervals. Note the smaller age range for females relative to males.

comparatively, because while numerous studies examined aging trends in various human athletic disciplines (Baker and Tang 2010 and references therein; Bernard et al. 2010) most of these studies do not include activity level or event frequency as a factor; indeed, professional athletes are typically used as subject for aging studies precisely because their activity levels are roughly comparable (Van Damme et al. 2002). Consequently, even though we have controlled for intrasexual playtime in the current study, the sex-specific aging trends may still be affected by differences in overall frequency and number of games played in the NBA versus the WNBA. Future studies examining effect of activity level on performance aging, both in humans and nonhuman animals, would be valuable for resolving this issue.

A final possible cause of the observed discrepancy in performance aging between males and females is sex-specific life-history trade-offs. Males and females frequently differ in the timing and extent of key resource allocation decisions, such as reproductive investment, which may be reflected in overall lifespan and aging (Bonduriansky et al. 2008). For example, a recent study on humans showed that female birth rate (i.e., the mean number of children produced by women aged 15–45 years old) explains a significant amount of the variation in sex differences in lifespan across human populations (Maklakov 2008). The extent to which such costly life-history events affect performance aging in particular, however, is unknown for any animal species. The relationships between whole-organism performance and life-history traits that might influence aging are little explored, but likely to be complex (S. P. Lailvaux and J. F. Husak, unpubl. data). The possibility that trade-offs might have shaped selection on aging patterns of performance in males and females, although having received little attention, cannot be ignored.

POINT TYPE

Males and females also differed in the observed patterns of aging for point type, as indicated by the interactions between sex, point type, and the nonlinear aging term in the best-fitting model (Table 2). Within males, the aging curves for points/min from two-point field goals and free throws are extremely similar to the curve for total points/min, with equivalent peaks at approximately age 25 (Figs. 1A and 2A). The aging curve for points/min from three-point field goals, however, is distinct, with a later peak at approximately age 30. The three-point field goal aging curve for females is also noticeably different from the other female curves, and females also exhibit a peak and subsequent decline in points scored from three-point field goals (Figs. 1B and 2B). However, the peak is much less clearly defined than in males, and the drop-off in three point field goals in also less marked in females relative to males. Our second hypothesis (i.e., that males and females compensate for reduced overall performance by exhibiting different patterns of aging) is, however, only partially supported.

The three-point field goal aging curves do indeed peak at a later age once the scoring rate for the other two point types has begun to decline. As a compensation mechanism, this makes sense—high-intensity, short duration muscle movements, such as those that power jumping, are achieved using type 2 muscle fibers that are especially subject to decline with age (Lexell and Downham 1992; Hawkins et al. 2003; Macaluso and De Vito 2004). Accuracy is a suitable compensatory performance trait that might offset this decline, as it would afford players an advantage in terms of three-point field goals at the same time that their two-point field goal scoring ability is on the wane. However, there is little evidence from our dataset to suggest that this shift in scoring proficiency compensates in terms of overall points scored. For both men and women, the total points/min aging curve is most similar to those for two-point field goals and free throws, suggesting that it is these two score types, rather than three-point field goals, that drive overall basketball scoring performance.

A further factor that might explain the disparities in point type aging between men and women is interactions between teammates, which may be a consequence of physical differences between the sexes (e.g., height, see below). Studies of aging in human performance thus far tend to center on performance in individual events or sports, such as track and field events, or on aspects of performance in team sports, such as baseball pitching, where individual performance is easily quantified and independent of the actions of teammates. However, the aging of performance in a team sport such as basketball could in principal be fundamentally different from that of individual events because the aging of some aspects of performance, and also compensation for that performance, could be modified, alleviated or obscured by what other players in the team are doing. Our analyses controlling for overall team "quality" suggest that the ability level of the team has no influence on performance aging in females, and only a marginal effect in males. But while the overall quality of a team might not influence performance aging, the way in which members of a team play the game might well do so. Indeed, males score at an average higher rate than females over the most of their careers (Figs. 1 and 2). Furthermore, although men on average tend to be taller than women—even in this specialized dataset (see Results)—the regulation basket height is the same in both the NBA and the WNBA (3 meters). "Dunking" the ball is therefore on average easier for males compared with females, and women would consequently tend to compensate for this difficulty by employing different game play strategies to men—thus, WNBA play is more likely to emphasize cooperation among players than NBA games, and this cooperation may again affect the age trajectory of a player's career. The question of whether individual aging in a given trait can be affected by what others in a population are doing is especially intriguing from an evolutionary ecology perspective, and might be highly relevant in species where cooperation among individuals can have important lifetime fitness effects. However, we are not aware of any studies that have examined group effects on trait aging in cooperative animal species.

Conclusions

Our analysis of over 30 years of data on performance in professional basketball players suggests that basketball performance in men and women is subject to different patterns of age-related change. This finding is similar to that of a recent study that also demonstrated sex-specific aging of multiple whole-organism performance in nonhuman animals (Lailvaux et al. 2011). With the exception of three-point field goals, which peak at approximately age 30, peak performance for male players is achieved at roughly age 25 and thereafter senesces. By contrast, the aging curves for female performance are significantly flatter, with no clear peaks. While our results hint at possible compensation for age-related drop-offs in performance, it is unclear whether such compensation (if any) is effective. Future studies examining the effect of activity level and teamwork on the aging of athletic traits would be valuable for understanding the behavioral and physiological responses to sex-specific aging in functional contexts.

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DATA ARCHIVING

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Supporting Information

Additional Supporting Information may be found in the online version of this article at the publisher's website:

Table S1. Best-fitting model describing the variation in the (total number of points scored/minute)$^{1/2}$ over individual playing careers by sex and age (in years), controlling for height (in cm) and team quality (% of games won in a given season).

Table S2. Best-fit model results for (points/min)$^{0.3}$ scored as a function of sex, age and point type (two pointers, three pointers, and free throws) over individual playing careers broken down by point type, in combination with sex and age (in years), and controlling for height (in cm) and team quality (% of games won in a given season).

Table S3. Best-fit model results for (points/min)$^{0.3}$ scored as a function of both age and point type for (a) males and (b) females and controlling for height (in cm) and team quality (% of games won in a given season).