Survival of the Fastest: The Multivariate Optimization of Performance Phenotypes

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ABSTRACT

CALSBEEK, R., and V. CAREAU. Survival of the Fastest: The Multivariate Optimization of Performance Phenotypes. *Med. Sci. Sports Exerc.*, Vol. 51, No. 2, pp. 330–337, 2019. **Introduction**: Trade-offs are widespread in biological systems. Any investment in one trait must necessarily limit the investment in other traits. Still, many studies of physiological performance produce positive correlations between traits that are expected to trade-off with one another. Here we investigate why predicted trade-offs may often go unmeasured in studies of human athletes. **Methods**: Triathletes compete in consecutive swimming, cycling, and running events as a single competition, events whose physical demands may be especially prone to generating performance trade-offs. Performance variation in these three events interacts to explain overall variation in athletic performance. **Results**: We show that individual variation in athletic performance can mask trade-offs among disciplines, giving the impression that high-performance triathletes are athletic generalists. Covariance in race performance across the three disciplines was positive in the most elite athletes but became increasingly negative as race times increased. **Conclusions**: These performance trade-offs among the disciplines preclude the realization of a generalist athlete except in the most elite triathletes, a result similar to the "big houses, big cars" phenomenon in life history evolution. This distinction between trait combinations that are favored for optimal performance versus constrained by trade-offs was only apparent when accounting for individual level variation in athletic performance. Our results provide further evidence that meaningful trade-offs may be missed if individual variation in quality is disregarded. **Key Words**: SPECIALIST, GENERALIST, PERFORMANCE, QUALITY, TRIATHLON

In 2005, American cyclist George Hincapie won stage 15 of the Tour de France. His victory came at the end of a race over six mountain passes, finishing on the summit of Pla d'Adet in the French Pyrennes. The win on Pla d'Adet was especially surprising given that Hincapie was previously known as a powerful sprinter who excelled in flat races over a single day, not a mountain specialist in a stage race. Allegations (1) of Hincapie's use of performance-enhancing drugs notwithstanding, the apparent absence of a performance trade-off runs counter to the idea (2) that allocation to one athletic discipline (e.g., sprinting) should detract from allocation to another discipline (e.g., climbing).

Despite evidence for the near ubiquity of trade-offs (3–5) and the important role they play in shaping life history evolution (6), trade-offs remain notoriously difficult to demonstrate in some circumstances (7). Previous studies of human athletes, for example, have provided mixed results in the study of performance trade-offs. Although morphological and physiological traits are subject to functional constraints that intuitively suggest trade-offs, numerous studies of human athletes have reported positive correlations among performance variables (8,9). This counterintuitive result has been explained as the result of interindividual variation in "quality" that may mask trade-offs within individuals. The importance of individual variation in quality remains contentious in human studies (10,11). Quality differences may be intrinsic (some athletes are morphologically better suited to some athletic events than others) or extrinsic (some athletes train harder or more efficiently than others), the latter source of variation being of prime interest in performance studies (11).

Another challenge in studying trade-offs in human athletes is the lack of a clear and quantitative measure of performance to discriminate among athletic performances of different types. For example, although decathletes compete in multiple events with different morphological and physiological demands, events are scored separately and on different scales before being combined into an overall score (11). Scoring is a historically variable process in the decathlon, and moreover, events scored by distance (e.g., throwing) versus time (e.g., running) are weighted differently (e.g., positive vs negative power functions which alter the detection probability for trade-offs). This lack of consistent performance metric across disciplines may

affect the comparison of performance variation among athletes with different specialties.

Human triathletes provide a unique opportunity to overcome several of the aforementioned challenges. Triathletes compete in consecutive swimming, cycling, and running races that are performed one after another as a single athletic event. Triathlons vary in total distance, and "Iron" distance triathlons are among the longest triathlons. In an iron distance triathlon, athletes swim 3.8 km, cycle 180 km, and run 42.2 km. Optimal performance in each discipline requires a unique set of morphological attributes and skill sets and differences in training regime. These alternative demands lead to a wide range of athletic abilities and specialties in triathletes, which should lead to the expression of performance trade-offs among disciplines. Each event time is added to the next, and overall race-time provides a graded evaluation of race performance. Race times therefore provide an unbiased estimate of performance that is scalable across the disciplines. Individual variation in "quality" may be particularly high in a data set of Ironman race times because each race includes professionals and amateurs from various age categories. Options for at least partially accounting for variation due to differences in quality include 1) grouping triathletes in increments of finishing race time (e.g., bins of progressively faster athletes within a race) and 2) using mixed models to analyze the among- and within-athlete correlations for cases in which athletes have multiple event records.

Here we test (a) whether such performance trade-offs are detectable in measures of Ironman triathlete performance, and if so, (b) whether performance trade-offs lead to generalist or specialist strategies in triathletes in general.

METHODS

Data description. We acquired data from the publicly available Ironman™ triathlon database at www.ironman.com. We compiled race results from 86 total Ironman™ triathlon events at 32 different venues held around the world during years 2013–2016 (see Table, Supplemental Digital Content 1, Descriptive statistics for raw data, http://links.lww.com/MSS/B397). We recorded demographic data for athletes, including sex, country of origin, and age category (here age category refers only to amateur athletes, and all professional triathletes are pooled irrespective of age). We also collected data for altitude at each race venue and elevation gain on the bicycle portion of the race. We included time spent swimming, cycling, and running and total race time, including the few minutes spent transitioning between events. We removed observations with a total race time greater than 17 h (most organized Iron distance events allow 17 h for an official race finish). We also removed any athlete's records with missing data for sex, athlete identity, time spent swimming, cycling, running, or total racing. We also removed obvious outliers for swimming, cycling, and running time. We removed observations from age categories that included <500 observations (F60–64, F65–69, F70–74, M60–64, M65–69, M70–74, M75–79, M80–84, and M80+). Finally, we removed observations from less popular races in which fewer

than 200 athletes competed (this occurred only in females, in 20 out of 86 races). This yielded a total of 149,291 observations on 110,134 athletes (27,269 and 122,022 observations on 20,166 women and 89,990 men, respectively; see Figure, Supplemental Digital Content 2, The frequency distribution of repeated measures, http://links.lww.com/MSS/B398).

We accounted for individual variation in "quality" in several ways: first, we created performance category "bins" for athletes separated by quantiles (i.e., 10 decile bins of equal numbers of athletes) for males and females in each race. Bins were used to create separate pools for analyses of variance–covariance matrices and for multivariate mixed models (see below). We also separated athletes in bins of finishing time (in 1-h increments). There were too few observations <10 h for females, so we pooled these observations into the 10- to 11-h time bin. We created different subsets of the data by progressively adding variation in final race time by these 1-h increments (e.g., finish times <9 h, <10 h, <11 h, etc.). Presumably, variation in quality will be lowest in the <9-h bin and will progressively increase as we introduce longer time into the data (e.g., the entire data set is included in the <17 h). Therefore, we expected that this would generate positive correlations where trade-offs are otherwise expected (akin to the "big houses big cars" scenario made by van Noordwijk and de Jong (12,13) in which although most individuals who purchase an expensive house are precluded from purchasing an expensive car, some individuals acquire a resource surplus sufficient to allocate across multiple aspects of their life history, thereby masking the allocation trade-off).

Multivariate mixed models. We estimated the among-individual correlation (r_{ind}) and the residual correlation (r_e) between swimming, cycling, and running performance by fitting multivariate mixed models using ASReml-R (14). We fit a separate model for each subset of the data according to final time category bins (see above). All traits were standardized (mean = 0, variance = 1) within each subset of the data. Division, altitude, and elevation gain were fitted as fixed effects in each model. Each multivariate model included two fully unstructured correlation matrices: one for the random effect of individual identity to model all among-individual variances and correlations (r_{ind}) and one for the residuals to model all within-individual variances and correlations (r_e). We used nadiv (15) to calculate the approximate 95% confidence intervals (CI) of all r_{ind} and r_e using profile likelihoods. Estimates whose 95% CI did not overlap with 0 were considered to significantly differ from zero.

The r_{ind} indicates consistent association between individual mean values for different traits over the time span within which the measures were taken. The r_{ind} is influenced by two main sources of among-individual covariance between traits: genetic and permanent environmental effects, both of which are likely to occur in the data. Indeed, the data set includes athletes from various countries showing large differences in environmental, cultural, and socioeconomic factors that may generate consistent among-individual differences in

performance. If one or more environmental factors consistently affect performance in more than one discipline, this would cause correlations at the among-individual level. Genetic correlations can also contribute to consistent covariation among traits through pleiotropy and linkage disequilibrium (16). If one or more genes affect performance in swimming, cycling, and running, this would cause correlations at the among-individual level (17,18).

The r_e indicates whether an athlete's change in performance in one discipline between time period t and $t + 1$ is correlated with its change in another discipline over the same period. One source of covariance at the residual level comes from correlated measurement error (19). However, given the precision of timing measurements in Ironman™ competitions, we consider correlated measurement error to be a negligible source of covariance. An r_e can also arise from combined, reversible changes between traits occurring within an athlete due to correlated phenotypic plasticity (20–22). This would occur if, for example, athletes change their swimming, running, and cycling performance as a function of an unidentified covariate (e.g., training regime, temperature, and nutritional status during the race). Moreover, an athlete that performs better than his or her own average early in the race may compromise their performance later in the race. For
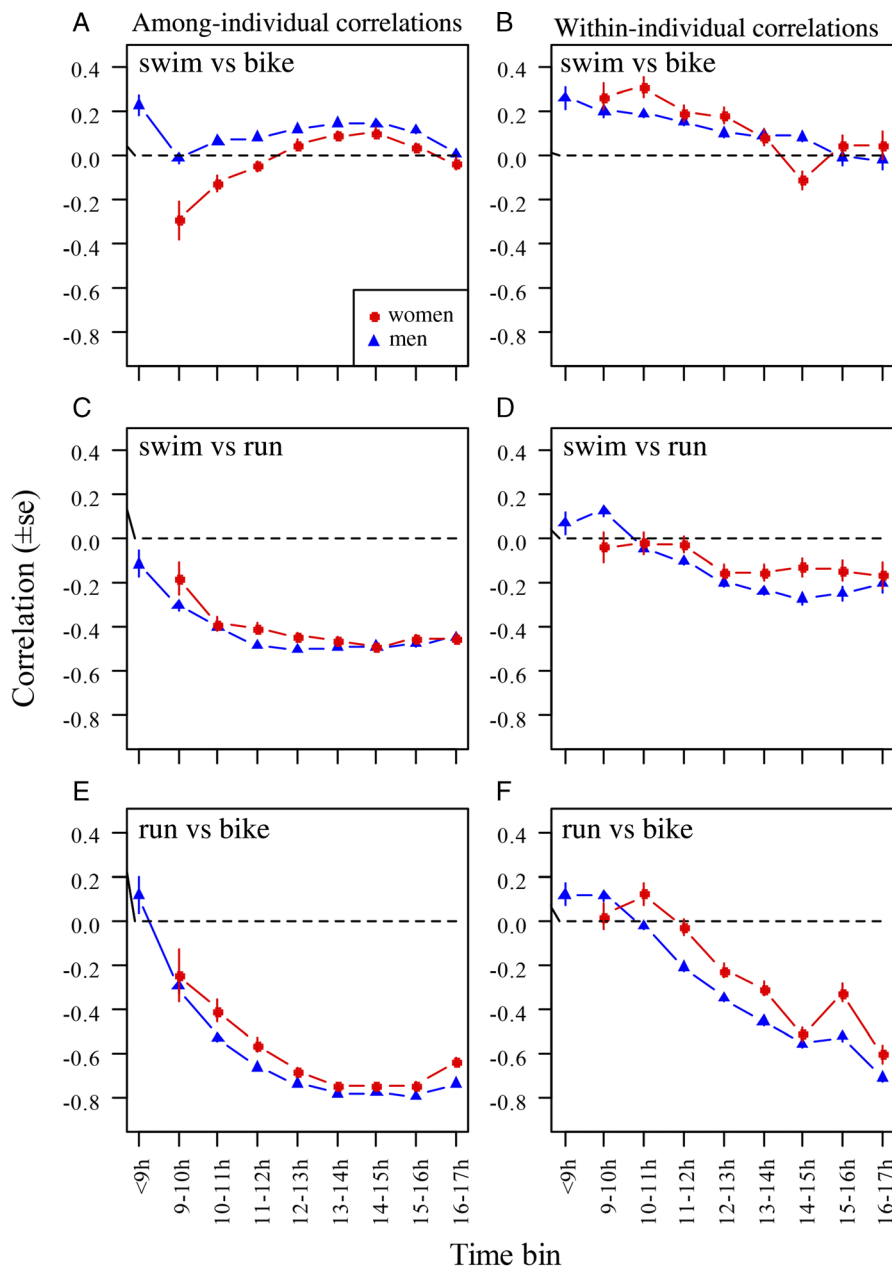

FIGURE 1—Slower athletes experience trade-offs. Correlations ± SE between swimming and cycling performance (A–B), swimming and running performance (C–D), and running and cycling performance (E–F) in 112,442 athletes that participated in 86 Ironman™ competitions throughout the world during 2013 to 2016. Correlations were estimated at the among-individual level (*left panels*) and the within-individual level (*right panels*), separately for males (*blue triangles*) and females (*red dots*) according to finish time bin (in 1-h increments).

example, larger workloads on the bicycle may compromise subsequent running performance (23), which would generate a negative r_e.

Performance gradient analysis. We applied a classic Lande and Arnold (24) style of statistical analyses to generate "performance gradients" (25,26) to measure the influence of swimming, cycling, running, and their interactions on overall race performance. All analyses were conducted separately for each sex and for each decile bin of each race. We used final race rank as a measure of "overall performance," standardizing each athlete's rank relative to the mean of their

finish time bin. Swimming, cycling, and running times were standardized to mean = 0 and SD = 1. We then performed multiple regressions using these standardized variables to extract linear performance gradients on each underlying performance metric. We ran separate multiple regression models using the data included in each bin, generating 86 and 56 estimates for each time bins in men and women, respectively. Because for this study we were explicitly interested in the nature of how performance trade-offs shape the nature of multitrait optimization, we also report the covariance matrices for each performance decile to illustrate covariation among
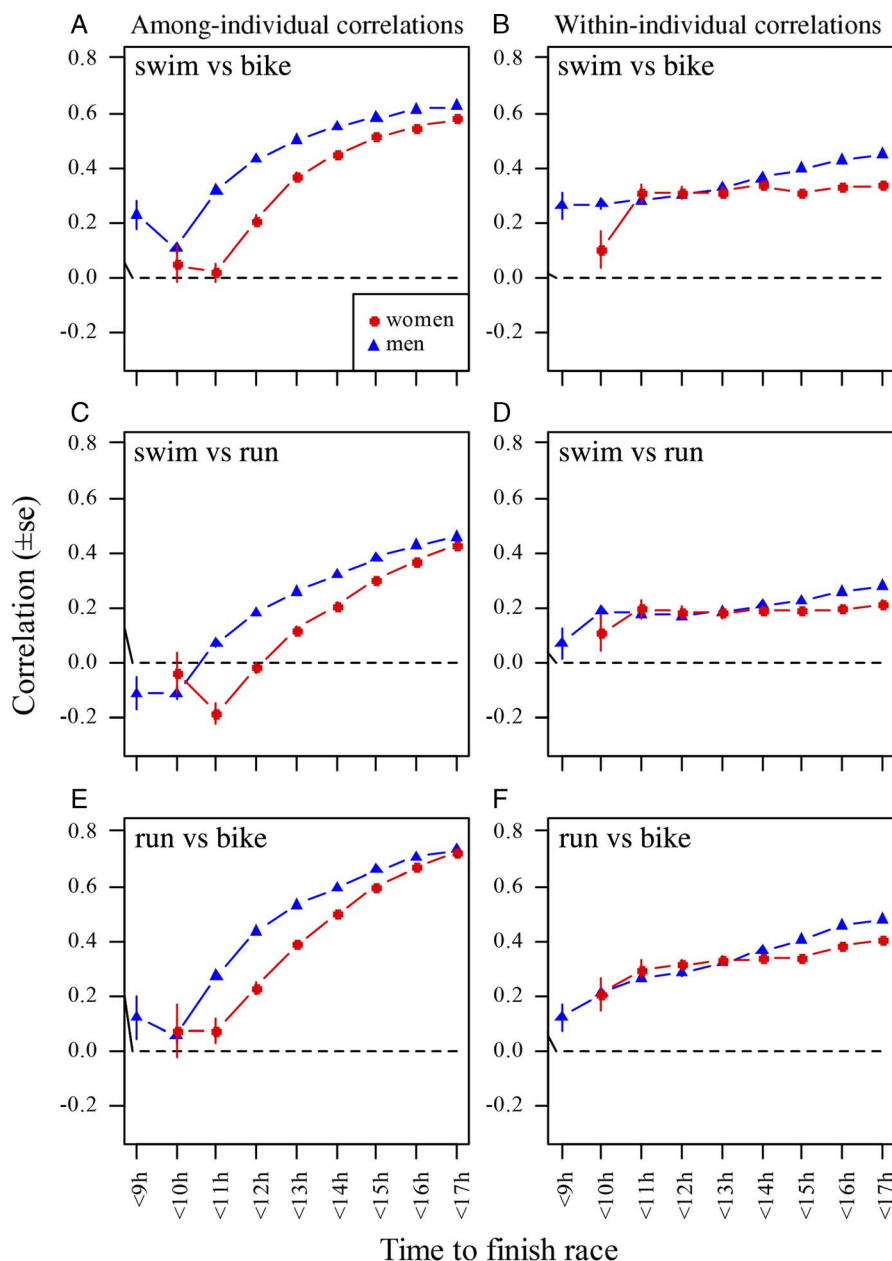

FIGURE 2—Variation in quality can generate positive correlations where trade-offs are expected. Correlations ± SE between swimming and cycling performance (A–B), swimming and running performance (C–D), and running and cycling performance (E–F) in 112,442 athletes that participated in 86 Ironman™ competitions throughout the world during 2013 to 2016. Correlations were estimated at the among-individual level (*left panels*) and the within-individual level (*right panels*), separately for males (*blue triangles*) and females (*red dots*) according to finish time. This figure shows that progressively adding variation in "quality" into the data set generates positive correlations among traits expected to show trade-offs.

pairwise trait combinations. Negative trait covariances indicate performance trade-offs across disciplines.

Finally, we fitted multivariate mixed models using ASReml-R (14) to test whether the among- and within-individual correlation matrices for swimming, cycling, and running times were different in the 0–10 and 10–20 decile bins. We used a log-likelihood ratio test to compare a full model allowing correlation matrices to differ versus a reduced model in which the among- or within-individual correlation matrices were constrained to be equal in the 0–10 and 10–20 decile bins. This test asks whether constraining trait correlations to remain the same across the top two decile bins produces a better fit than a model that relaxes this constraint.

As a complementary approach to the analysis of linear performance gradients and trait covariances, we also estimated correlational (multivariate) performance gradients (25). Correlational performance gradients are measured statistically as the pairwise interaction between traits in a full factorial model that also includes linear and quadratic terms. Standard multivariate regression underestimates the correlational performance gradients (and their standard errors) by a half, as is the case for estimates of the strength of natural selection (27). Thus, all coefficients and standard errors were doubled for presentation. The total variance explained by correlational performance models was small relative to the linear performance gradients but for completeness we provide these results as an appendix.

RESULTS

Among- and within-individual correlations. Multivariate mixed models revealed multiple trade-offs at the among- and within-individual individual levels in the different time bins (Fig. 1). Moreover, the patterns were similar in male and female triathletes. Overall, there was no trade-off between swimming versus cycling performance at both the among- and within-individual levels (Fig. 1A and B). Except for women in the 10- to 11-h time bin (Fig. 1A), all r_{ind} were either nonsignificantly different from 0 or positive. The r_e values were positive and significant in shorter time bins and became progressively closer to 0 in longer time bins (Fig. 1B). By contrast, there were clear trade-offs between swimming versus running (Fig. 1C and D) and running versus cycling performance (Fig. 1E and F). For both pairs of traits, there was no trade-off in the fastest time bin, but the r_{ind} became progressively more negative and significant in longer time bins in both men and women (Fig. 1C and E). Interestingly, the same pattern occurred at the within-individual level, as the r_e was close to 0 in the fastest time bins but became progressively more negative in longer time bins (Fig. 1D and F). The negative r_{ind} indicates that athletes that are consistently faster than average in cycling tend to consistently perform slower than average in running. The negative r_e indicates that an athlete performing faster than its average during cycling on a given competition will tend to perform slower than its average during running of that same competition.

Results were strikingly different when analyses were based on subsets of the data that progressively added variation in final finish time (i.e., <9 h, <10 h, <11 h, and so forth instead of mutually exclusive bins like <9 h, 9–10 h, 10–11 h, and so forth). Indeed, although the <9- and <10-h bins yielded similar results, both the r_{ind} and the r_e became progressively positive as more variation in final race time is included in the analyses (Fig. 2). Finally, the analysis conducted separately within each division yielded positive correlations in all cases (see Figure, Supplemental Digital Content 3, Lack of apparent trade-offs within divisions, http://links.lww.com/MSS/B399), suggesting that
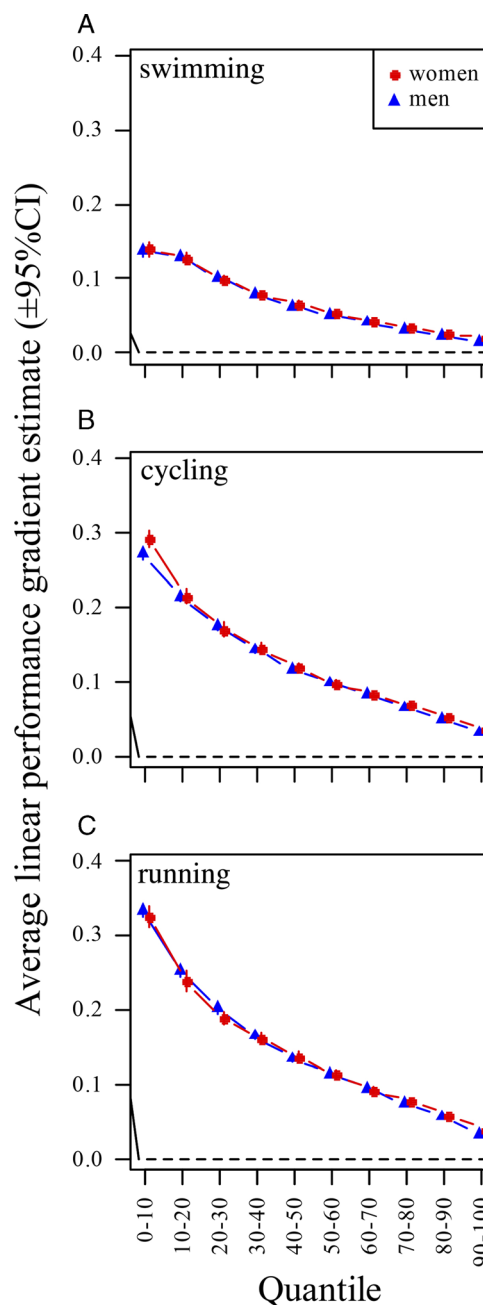

FIGURE 3—Linear performance gradients ± SE for swimming (A), cycling (B), and running performance (C), separately for men and women in each time bin.

there is enough variation within division to mask potentially important trade-offs.

Performance gradients and trait covariance. Although performance gradients were positive for all events and for all performance deciles, the magnitude of these gradients varied with athletic "quality" (Fig. 3). Linear performance gradients were weakest in the slowest athletic deciles and grew progressively stronger in faster deciles across all three disciplines (Table 1). Similarly, covariance structure varied among performance deciles (Table 2). The fastest athletes tended to have weakly positive covariance between performance measures, but these covariances became strongly negative as athletic "quality" declined. Results were similar for males and females and across the three pairwise combinations of athletic discipline. Correlational performance gradients were largely consistent with the patterns of trait covariance (see Figure, Supplemental Digital Content 4, Correlational performance gradients, http://links.lww.com/MSS/B400). In particular, both males and females in the 9- to 10-h finish time bins had the largest positive correlational performance gradients for swimming–cycling and for swimming–running. Nearly all of the correlational performance gradients were significant for male athletes that finished in the 9- and 10-h time bins and the number of significant gradients declines in subsequent bins (see Table, Supplemental Digital Content 1, Descriptive statistics for raw data, http://links.lww.com/MSS/B397). Patterns were qualitatively similar in females, although fewer total correlational performance gradients were statistically significant.

DISCUSSION

We have shown that athletic performances across the three disciplines of triathlon tend to be positively correlated in elite athletes and that these positive correlations break down with increasing race times. Performance correlations closely mirrored the patterns revealed in trait covariances: high-performance values improve finishing race rank across all three disciplines but only among the fastest athletes in the data set. Together these results suggest that generalist athletes are favored in Ironman triathlon but that allocation-based trade-offs preclude the generalist strategy in all but the fastest athletes.

There are several possible ways, both intrinsic and extrinsic, in which individual variation in "quality" could mask trade-offs experienced by triathletes (11). Functional trade-offs related to "intrinsic" differences in morphology may generate trade-offs if, for example, the broad shoulders and increased body mass favored in elite swimmers compromises aerodynamic efficiency on the bicycle. We find poor support for this hypothesis, however, because the correlations between swimming and cycling performance remain positive over a larger range of finishing times (Fig. 1B) compared with other pairwise performance correlations. Allocation based trade-offs are an

TABLE 1. Average linear performance gradients (β) for swimming, cycling, and running performance, separately for men and women in each time bin.

Decile	Men			Women		
	β	95% CI		β	95% CI	
		Lower	Upper		Lower	Upper
(A) Swimming						
0–10	0.272	0.263	0.281	0.291	0.280	0.302
10–20	0.214	0.207	0.221	0.214	0.204	0.224
20–30	0.174	0.169	0.179	0.170	0.161	0.179
30–40	0.143	0.139	0.147	0.145	0.139	0.151
40–50	0.116	0.113	0.120	0.118	0.112	0.123
50–60	0.098	0.095	0.101	0.096	0.092	0.101
60–70	0.082	0.079	0.085	0.082	0.079	0.086
70–80	0.065	0.063	0.067	0.067	0.065	0.070
80–90	0.049	0.047	0.051	0.053	0.050	0.055
90–100	0.030	0.029	0.032	0.036	0.033	0.038
(B) Cycling						
0–10	0.334	0.325	0.343	0.326	0.312	0.339
10–20	0.252	0.246	0.259	0.238	0.225	0.252
20–30	0.202	0.195	0.209	0.188	0.179	0.198
30–40	0.165	0.160	0.170	0.162	0.155	0.169
40–50	0.134	0.131	0.138	0.137	0.130	0.143
50–60	0.114	0.111	0.118	0.113	0.107	0.118
60–70	0.095	0.092	0.098	0.092	0.088	0.096
70–80	0.075	0.073	0.077	0.077	0.074	0.080
80–90	0.057	0.055	0.059	0.059	0.056	0.062
90–100	0.033	0.032	0.035	0.040	0.037	0.042
(C) Running						
0–10	0.137	0.130	0.144	0.139	0.129	0.148
10–20	0.130	0.125	0.134	0.127	0.121	0.134
20–30	0.102	0.098	0.106	0.099	0.094	0.104
30–40	0.079	0.076	0.082	0.079	0.075	0.082
40–50	0.063	0.061	0.065	0.066	0.063	0.070
50–60	0.051	0.049	0.052	0.053	0.051	0.056
60–70	0.041	0.039	0.043	0.042	0.040	0.044
70–80	0.031	0.030	0.033	0.034	0.032	0.036
80–90	0.023	0.022	0.024	0.027	0.026	0.029
90–100	0.015	0.014	0.016	0.019	0.018	0.021

The average gradient and 95% CI were calculated based on gradients estimated within each decile time bin for each race.

| Bin | | Among-Individual Variance–Covariance Matrix | | | | | | Within-Individual Variance–Covariance Matrix | | | | | |
| | | Men | | | Women | | | Men | | | Women | | |
		Swimming	Cycling	Running	Swimming	Cycling	Running	Swimming	Cycling	Running	Swimming	Cycling	Running
0–10	Swimming	0.746	0.071	−0.055	0.832	−0.013	−0.091	0.118	0.041	0.027	0.108	0.049	0.040
0–10	Cycling	0.071	0.513	0.019	−0.013	0.514	−0.032	0.041	0.243	0.069	0.049	0.279	0.117
0–10	Running	−0.055	0.019	0.456	−0.091	−0.032	0.409	0.027	0.069	0.394	0.040	0.117	0.422
10–20	Swimming	0.884	−0.003	−0.375	0.909	−0.064	−0.347	0.117	0.006	−0.033	0.075	0.029	−0.003
10–20	Cycling	−0.003	0.725	−0.482	−0.064	0.755	−0.488	0.006	0.281	−0.093	0.029	0.250	−0.057
10–20	Running	−0.375	−0.482	0.668	−0.347	−0.488	0.730	−0.033	−0.093	0.331	−0.003	−0.057	0.286
20–30	Swimming	0.878	0.000	−0.418	0.934	−0.025	−0.392	0.122	0.014	−0.046	0.065	0.009	−0.020
20–30	Cycling	0.000	0.816	−0.614	−0.025	0.827	−0.626	0.014	0.191	−0.110	0.009	0.186	−0.098
20–30	Running	−0.418	−0.614	0.784	−0.392	−0.626	0.834	−0.046	−0.110	0.224	−0.020	−0.098	0.205
30–40	Swimming	0.854	0.051	−0.429	0.963	0.033	−0.436	0.145	−0.011	−0.039	0.066	0.003	−0.029
30–40	Cycling	0.051	0.789	−0.653	0.033	0.888	−0.727	−0.011	0.218	−0.136	0.003	0.128	−0.065
30–40	Running	−0.429	−0.653	0.819	−0.436	−0.727	0.902	−0.039	−0.136	0.193	−0.029	−0.065	0.136
40–50	Swimming	0.887	0.046	−0.428	0.982	−0.006	−0.435	0.113	0.008	−0.050	0.046	0.009	−0.023
40–50	Cycling	0.046	0.806	−0.663	−0.006	0.907	−0.719	0.008	0.201	−0.140	0.009	0.114	−0.086
40–50	Running	−0.428	−0.663	0.819	−0.435	−0.719	0.898	−0.050	−0.140	0.194	−0.023	−0.086	0.141
50–60	Swimming	0.906	0.099	−0.465	0.934	0.063	−0.473	0.098	0.002	−0.035	0.068	0.003	−0.023
50–60	Cycling	0.099	0.818	−0.688	0.063	0.911	−0.744	0.002	0.182	−0.131	0.003	0.120	−0.077
50–60	Running	−0.465	−0.688	0.840	−0.473	−0.744	0.918	−0.035	−0.131	0.170	−0.023	−0.077	0.118
60–70	Swimming	0.861	0.078	−0.427	0.920	0.037	−0.423	0.140	0.020	−0.062	0.087	−0.002	−0.034
60–70	Cycling	0.078	0.783	−0.666	0.037	0.904	−0.758	0.020	0.214	−0.150	−0.002	0.123	−0.064
60–70	Running	−0.427	−0.666	0.813	−0.423	−0.758	0.927	−0.062	−0.150	0.196	−0.034	−0.064	0.103
70–80	Swimming	0.886	0.092	−0.427	0.935	0.068	−0.442	0.121	0.017	−0.049	0.062	−0.014	−0.015
70–80	Cycling	0.092	0.782	−0.652	0.068	0.958	−0.795	0.017	0.216	−0.152	−0.014	0.070	−0.027
70–80	Running	−0.427	−0.652	0.802	−0.442	−0.795	0.971	−0.049	−0.152	0.204	−0.015	−0.027	0.073
80–90	Swimming	0.868	0.125	−0.429	0.927	0.087	−0.440	0.133	0.004	−0.044	0.081	−0.015	−0.014
80–90	Cycling	0.125	0.776	−0.631	0.087	0.751	−0.611	0.004	0.225	−0.120	−0.015	0.264	−0.163
80–90	Running	−0.429	−0.631	0.815	−0.440	−0.611	0.832	−0.044	−0.120	0.193	−0.014	−0.163	0.199
90–100	Swimming	0.822	0.075	−0.321	0.937	−0.032	−0.368	0.188	0.042	−0.031	0.093	0.009	−0.012
90–100	Cycling	0.075	0.640	−0.397	−0.032	0.755	−0.492	0.042	0.364	−0.096	0.009	0.267	−0.108
90–100	Running	−0.321	−0.397	0.719	−0.368	−0.492	0.802	−0.031	−0.096	0.285	−0.012	−0.108	0.225

alternative and more likely "extrinsic" explanation. We suggest that training status of the fastest athletes allows them to perform at a high level in one discipline (e.g., cycling) and retain sufficient energetic resources to also perform well in subsequent disciplines (e.g., running). By contrast, less-trained athletes may readily over tax themselves in one discipline to the detriment of subsequent disciplines. This may explain why we see stronger trade-offs associated up with the running discipline, which occurs last and at the point of greatest fatigue. By contrast, cycling is involved in weaker trade-offs, perhaps because the bicycle itself provides both aerodynamic and mechanical advantages that can compensate for some of variation in quality, especially among the slowest athletes (also see below for a discussion on the negative within-individual correlations). This is consistent with the view that variation in resource acquisition can lead to changes in life history trade-offs (the so-called big houses, big cars argument (12,13) in which some individuals acquire a resource surplus that is sufficient to mask allocation trade-offs).

The observation that individual variation in quality affects the ability to detect performance trade-offs is not new. Previous studies of Olympic decathletes have suggested that controlling for "quality" reveals the expected negative correlations among throwing, jumping, and running performance (8,9). Although the idea is simple and intuitive, how to properly control for "quality" is a subject of debate (11). Most recently, Careau and Wilson (10) showed that trade-offs can be detected in decathletes and heptathletes—without the need to control for quality—by considering all repeated measures in a multivariate mixed model analysis. Their analyses, however, were restricted to a subset of athletes that were themselves drawn from a highly select subpopulation (elite generalist athletes). By contrast, the Ironman data set analyzed here includes athletes with much wider range of age, athletic capacities, motivation, and total time spent training. This interesting property of the data set allowed us to progressively add slower and slower athletes (in 1-h finish time bins) to estimate the effect of variation in quality on performance correlations. As expected, doing so generated positive among-individual correlations (Fig. 2). This analysis illustrates that individual variation in athletic performance can mask trade-offs and failure to consider the effect this has on data structure might lead to the erroneous conclusion that all triathletes are generalists. However, one must be aware that culling data according to overall performance score (here final time) introduces other problems, largely surrounding statistical distributions of data (11,28), and more work is needed to better understand how to analyze performance data.

The importance of individual variation in quality also helps explain the result that the covariance structure of the data only reveals high-performance across all three disciplines in the fastest athletes. Slower athletes may not be favored to perform at maximal levels in all three events if allocation trade-offs impose too great a cost in overall performance. For example, excessive exertion while cycling is known to have a dramatic and negative effect on energy reserves left for the run (23). Interestingly, athletes with finish time above 12 h show negative within-individual correlation between cycling and running performance (Fig. 1F), supporting the presence of strong allocation trade-off. By contrast, fast athletes finishing in less than 12 h do not show such a negative within-individual

correlation (Fig. 1F). Indeed, elite triathletes experience relatively small reduction in running efficiency after cycling (29) likely owing to superior physiological condition that leave additional resources for the run. If this difference does indeed arise due to difference in physiological status, then plasticity in performance that arises through enhanced physical condition may underlie the generalist triathlete phenotype.

Differences in performance across multiple enviornments (or over time) involves multiple traits subject to optimization (30). Changing competitive context (e.g., water vs land) may further obfuscate trade-offs (31–33). We suggest that a fuller understanding of the importance of specialization should include a mixed perspective based on the individual variation in quality, the strength and form of performance gradients, and the genetic constraints (34) that ultimately shape trait correlations.

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