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MINI-REVIEW

Experiments of Nature

Natural experiments in marathon running

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Abstract

Natural experiments are a form of passive experiments that analyze populations exposed to environmental or behavioral stimuli. Here, we review natural experiments using marathon running as an example of an unusual physiological stressor to illustrate how such approaches can generate new hypotheses or test competing ones using large datasets of training and performance data. Natural experiments have been able to demonstrate that marathons are completed close to, but below, critical speed and that faster athletes complete marathons at a higher fraction of critical speed compared with slower runners. Environmental conditions, such as heat and altitude, as well as training and racing behaviors, including the characteristics of training programs and pacing strategies, have also been demonstrated to impact marathon performance. Findings from the natural experiments discussed herein often align with results from smaller, laboratory-controlled studies. However, the scale of these datasets has allowed for the detection of subtle trends and interactions that otherwise would remain undetected in smaller cohorts. In conclusion, natural experiments have helped advance our understanding of marathon physiology and can effectively complement traditional laboratory-based interventions. Future research may explore hybrid approaches in which researchers conducting well-controlled laboratory experiments collaborate with running platforms to design integrated research studies that combine large sample sizes with laboratory-controlled interventions.

big data; endurance; marathon

INTRODUCTION

Passive experiments are defined as studies with little or no active intervention from the investigator, typically on individuals exposed to unique or unusual physiological stressors (1). Passive experiments can be further classified as experiments of nature and natural experiments. The former examines individuals with rare genetic or acquired conditions, such as McArdle disease, whereas natural experiments analyze datasets from populations that differ in their exposure to environmental or behavioral stimuli, enabling researchers to measure specific outcomes and test targeted hypotheses (1).

Exercise, in its broad definition of any form of physical activity that aims to improve performance or health (2), can hardly be considered a unique physiological stressor (3). However, under certain circumstances, exercise might be considered a unique physiological stressor and thus be used to conduct natural experiments. For instance, the physiological effects of regular exercise over relatively short time periods (weeks to months) are well documented. However, studies investigating the effects of long-term exercise interventions (years to decades) are scarce and remain unusual, and natural experiments reporting fitness data across the lifespan have been used to bridge this gap (1).

Marathon running has experienced an increase in popularity over the past few years. Applications for the London Marathon increased from 247,069 in 2016 to nearly 1.4 million for the 2027 ballot. However, despite this growing interest, running a marathon remains a relatively rare feat. Less than ~0.005% of the global population takes part in one of the seven World Marathon Majors each year, and it has been estimated that <1% of the population has completed a marathon in the past 5 years (4). Therefore, despite humans exhibiting evolutionary traits that favor marathon running (5) and the recent increase in popularity, running a marathon can be considered an unusual physiological stressor.

Much of the research on endurance running has aimed to understand and expand the limits of human performance (6–8). Studies of marathon performance typically rely on laboratory tests to measure physiological or biomechanical markers of performance, even though recent research is starting to incorporate field-based measures (9, 10). Laboratory testing

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can be expensive and time-consuming, with modest ecological validity. In addition, elite athletes are, by definition, a small population (11), so research studies requiring athletes to modify their training programs before a major competition can be challenging (12). This is particularly the case if athletes are asked to be exposed to a condition or practice with the potential to have a deleterious effect on performance.

Endurance athletes often monitor performance and physiological responses during training and competition using devices that collect an increasingly wide range of variables, including metrics related to external workload, such as speed, altitude, or acceleration (13), and physiological parameters, including heart rate (HR) and heart rate variability (14), breathing frequency (15), interstitial glucose (16) and lactate concentrations (17), or sleep (18). These data are then uploaded to online platforms, enabling athletes and coaches to manage and design training programs (e.g., TrainingPeaks), monitor progression, or predict future performance. In turn, these platforms collect large sets of training, physiological, and performance data from thousands of athletes. For example, >10 billion exercise activities are now uploaded per year to Strava alone (19).

Given marathons are relatively unusual physiological stressors and performing laboratory-controlled studies is challenging, natural experiments using wearable-derived endurance training and racing data can be used to test and generate hypotheses. The aim of this review is to highlight the potential of performance and physiological data to generate new and test existing hypotheses, specifically relating to exercise physiology and marathon performance. First, we focus on how large datasets have been used to further the understanding of physiological factors underpinning marathon performance. Second, we investigate how large datasets of running data can be used to establish the effect of environmental factors, such as weather and altitude, and how behaviors, such as training and pacing strategies, can affect marathon performance. The final section of the paper will outline the practical applications, limitations, and future research in this field, highlighting the potential of combining passive experiments, typically retrospective analysis of existing data, with prospective experiments where certain hypotheses are tested. Although the focus of the review is on marathon performance as an exemplar, evidence drawn from other sports or events has been included where appropriate.

FORMULATING AND TESTING HYPOTHESES THROUGH TRAINING DATA

Markers of Marathon Performance from Training Data

Running a marathon requires a metabolic steady state to be maintained throughout virtually the entire race. If exercise is performed in the severe domain, steady-state metabolism cannot be maintained (20, 21), as the resynthesis of ATP through oxidative phosphorylation of fats and carbohydrates is not sufficient to satisfy the energetic demand. Exercise in the severe domain is therefore characterized by a substantial physiological perturbation at local and systemic levels (21), including depletion of phosphocreatine, accumulation of hydrogen ions and inorganic phosphate, and inexorable increases in oxygen uptake, culminating in exercise cessation within a few minutes (see, for a review, Ref. 22). The best performance in a marathon is, therefore, likely to be at the intensity corresponding to, or very close to, the maximal metabolic steady state.

There has been substantial interest in how the maximal metabolic steady state can be determined. Despite some controversy (23, 24), the asymptote of the speed-duration relationship, critical speed (CS), is generally accepted to represent the speed corresponding to the maximal metabolic steady state (25–27). A frequent criticism of CS is the time-intensive protocol it requires. The "gold-standard" protocol to determine CS involves multiple maximal efforts at slightly different intensities within the severe exercise domain, intended to result in a range of test durations of ~2–15 min (27, 28). The speed and duration of these tests are then used to construct the speed-duration relationship, from which CS is derived. Several alternative approaches have been proposed to estimate CS (29, 30), including an analysis of the best performance observed over a range of distances, where the relationship between speed and duration is constructed from the observed best efforts, instead of the maximal effort attained during a testing session(s).

Some studies have used training and performance data to determine CS in marathon runners. For example, Jones and Vanhatalo (31) reported that elite athletes complete the marathon at virtually the speed corresponding to their CS (~96%). Using a large dataset of training data, it was possible to test the hypothesis that training data during the weeks leading up to a major marathon could be used to estimate CS (32). The authors reported that, in >25,000 runners, the best performances over distances from 400 to 5,000 m recorded during training were used to determine CS, with models that generally had a good fit ($R^2 > 0.99$), suggesting that CS can be predicted with reasonable accuracy from training data. Furthermore, CS derived from training data predicted performance with ~7.7% error (32). On average, runners completed the marathon at ~85% of their predicted CS, irrespective of their sex or age (>40 vs. <40 yr). However, there was substantial variation depending on the marathon speed. The fastest runners in this dataset completed the marathon at >90% CS, but the fraction of CS at which runners completed the marathon decreased in a linear fashion with marathon finishing time. This relationship persists when considering the fraction of CS at which elite male and female athletes complete marathons (Fig. 1).

The finding that faster runners also sustain a higher fraction of CS throughout the marathon may be explained by a superior capacity to preserve physiological function during exercise (33–35). Indeed, the ability to preserve physiological function from deteriorating during prolonged exercise has been defined as "durability" (36) or "resilience" (37). Although there are ongoing discussions to establish clear definitions of these terms, for the purpose of this article, we will define durability as the ability to resist deterioration in physiological characteristics over time during prolonged exercise (38). There appear to be several methodological considerations that can influence the assessment of durability (39). One potential method to assess durability is by monitoring the ratio between internal workload (e.g., heart rate, HR) and external workload (e.g., speed) during prolonged exercise (36, 39, 40). A greater magnitude of decoupling between internal and external workloads is associated with worsened durability, as assessed via laboratory-based measurements of work rates at the intensity domain transitions before and after

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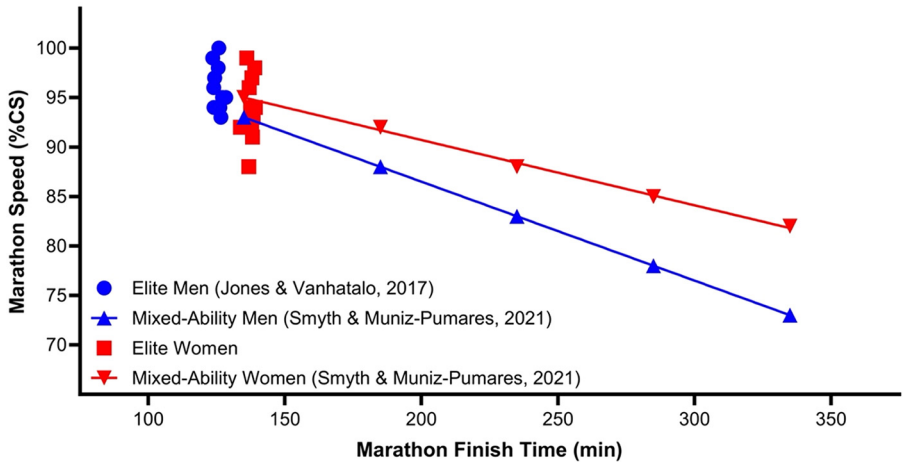

Figure 1. Marathon speed, expressed as a percentage of the athlete's estimated critical speed (% CS). Triangles show data obtained from ~18,000 male and ~6,000 female recreational runners, and data in circles and squares represent 12 elite male and female athletes, respectively. CS was determined from personal bests in elite athletes (31) and from the best performance recorded during training in recreational runners (32). The ability of athletes with faster finishing times to complete the marathon closer to their critical speed could be explained by their superior durability.

prolonged exercise (40). The hypothesis that decoupling of heart rate-to-speed ratio during a marathon contributes to explain performance in marathon running was tested by Smyth et al. (41). In this natural experiment, athletes who demonstrated high decoupling, defined as a heart rate-to-speed ratio ≥1.3 at the end of the marathon, relative to the 5–10 km segment (i.e., a ≥30% increase), completed the marathon in 3 h 58 min, compared with 3 h 37 min in athletes who exhibited low decoupling (i.e., a ratio <1.1). Furthermore, the authors reported that a regression model containing CS alone could predict marathon performance with an error of ~6.5% (41), comparable with the prediction error reported in a previous analysis (~7.7%; see Ref. 32). However, incorporating the magnitude of decoupling reduced the error in the prediction of marathon performance from ~6.5% to ~5.2%.

The approach taken in these experiments assumes that the best performance over certain distances recorded over a specific period of time [e.g., 16 wk before the marathon in the studies by Smyth et al. (32)] closely matches the performance observed during "intentional" maximal efforts. It should be highlighted that relying on performance data such as personal bests may overestimate CS by including performance no longer feasible for an athlete, whereas using training data may underestimate CS as it assumes the best observed performance represents a maximal effort. Nonetheless, good agreement between the best observed performance during training and the performance attained during intentional maximal efforts has been reported (30). Therefore, although the gold standard for CS estimation should require an athlete to perform intentional maximal efforts (28), the natural experiments presented herein suggest that training and performance data may provide reasonable predictions of performance, particularly for recreational runners, and further the understanding of physiology underpinning marathon performance.

Factors Affecting Marathon Performance: Environmental Conditions and Running Behaviors

Large datasets containing training and performance data may also be valuable tools to perform natural experiments, investigating individuals undertaking the same physiological challenge (e.g., running a marathon) but facing different constraints (e.g., environmental conditions), or to investigate how different behavioral strategies (e.g., pacing, training strategies) affect marathon performance.

Environmental conditions and marathon performance.

Performance is affected by environmental factors. For example, as the partial pressure of oxygen decreases with altitude, performance in events that rely on oxidative phosphorylation, such as the marathon, rapidly deteriorates. This can be illustrated by the results from the 1968 Olympic Games in Mexico City, which were held at an altitude of 2,240 m above sea level. Mamo Wolde won the gold medal for the marathon with a time of 2:20:26, which was ~8% slower than the world record at that time, held by Derek Clayton with a time of 2:09:36. (Of note, the first women's Olympic marathon was held at the 1984 Summer Olympics in Los Angeles.) This pattern was consistent across other endurance and long-distance events, and no new world records were set in any endurance discipline. In contrast, 24 athletic world records were set in the 1968 Olympic Games in Mexico City in short-distance track and field events due to the lower air resistance at altitude. Hamlin et al. (42) investigated the performance of 1,889 elite athletes at 794 venues, with a total of 132,104 track and field events analyzed. The results revealed that endurance performance in long-distance track and field running events (i.e., up to 10,000 m) was negatively affected even at very modest altitudes of 150–299 m above sea level, and this deterioration rapidly accelerates as altitude increases above 1,000 m. In marathon running specifically, a study of 1,280 performances observed in the top finishers from 16 races at altitudes from sea level to 2,800 m above sea level reported a negative correlation between marathon performance and altitude, though this was only evident at altitudes of over 700 m (43). The authors reported that for every 100 m above sea level, marathon performance decreased by ~1%. These studies demonstrate that marathon performance is highly sensitive to altitude and suggest that marathon performance will not be optimal in cities located at relatively modest elevations, such as Munich (~500 m) or Madrid (~650 m).

Weather conditions are also known to influence performance outcomes. Early laboratory-based studies reported an inverted U-shape relationship between ambient temperature and performance, with mild temperatures of 10°C–20°C suggested as optimal for endurance performance (44). Natural experiments, however, have further advanced our understanding of the extent to which environmental conditions affect marathon performance. Mantzios et al. (45) investigated the effects of weather parameters on endurance running performance in

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7,867 elite athletes competing across 1,258 races in 42 countries. The authors were able to establish that the "optimal" conditions for peak performance occur at 7.5°C–15°C wet-bulb globe temperature (or 10°C–17.5°C air temperature). In marathon running specifically, the best performance was reported at a wet-bulb globe temperature of 7.5°C. These results are in agreement with previous studies looking at performance in major marathons, which demonstrate a progressive deterioration of marathon performance as wet-bulb globe temperature increases from 5°C to 25°C (46). The negative effect of increasing temperature on marathon performance appears to be consistent both across different locations and within individual races, such as the Berlin (47), Boston (48), or New York Marathon (49). Further to its effect on marathon performance, natural experiments have been used to establish the effect of environmental conditions on the incidence of exertional heat stroke during a marathon, a serious and potentially life-threatening medical complication. Breslow et al. (50) reported that between 2015 and 2019, there were 3.7 cases of heat stroke per 10,000 marathon starters, but younger and faster runners had a higher risk, and greater increases in heat stress from start to peak during a marathon may exacerbate risk. These findings should be considered not only to adjust predictions of performance, but also by race management teams when establishing a "do-not-start" criteria to safeguard athletes in endurance events such as the marathon (51).

Endurance events, including Olympic Games and major city marathons, are typically hosted by large cities, where levels of pollution might be high. These events are often scheduled in the morning to avoid peak heat during midday hours, yet this might coincide with rush hour and potentially the highest levels of pollution [see Mougin et al. (52) for a review]. This is significant because air pollution may also affect endurance performance. Well-controlled randomized studies investigating pollution levels on performance, however, may not be feasible or ethical, due to the potentially harmful effects of pollutants on health. Fine airborne particulate matter smaller than 2.5 μm in diameter ($PM_{2.5}$) is produced during fuel combustion processes and can cross the lung-blood barrier and enter the bloodstream, where it can trigger inflammation in various tissues (53). Some studies have reported that high levels of $PM_{2.5}$ can impair airway function, which may in turn impact performance (54). An analysis of the top three athletes from seven competitive US marathons (168 race-years) revealed that, in women, for every 10 $\mu g \cdot m^{-3}$ increase in PM_{10}, marathon performance was decreased by 1.4%, even though air pollutants rarely exceeded the health limits (55). A criticism of the earlier studies was that air pollution was determined from monitoring stations, which may be far from the racecourses. More recently, $PM_{2.5}$ was estimated for 140 event-years (2.5 million marathon finishers) using a high-resolution machine-learning model that reconstructs $PM_{2.5}$ concentrations at specific locations such as marathon courses (56). Greater $PM_{2.5}$ exposure was associated with slower marathon times, with an increase of 1 $\mu g \cdot m^{-3}$ associated with ~30 s slower marathon (32 s in men, 25 s in women) (56). Overall, these natural experiments offer insight into the negative effects that air pollution has on marathon performance, with a level of sensitivity that would be very difficult to achieve through traditional laboratory interventions.

Pacing strategies and marathon performance.

Pacing refers to how athletes distribute energy and regulate effort and intensity to optimize performance (57). In endurance events, particularly long-distance races, it is generally accepted that an even-pacing strategy is optimal for performance. Studies investigating pacing strategies and marathon performance suggest that females and more experienced runners are more likely to adopt an even-pacing strategy compared with males and younger runners, who are more likely to adopt a positive split, i.e., starting fast in the first half before slowing down in the second half of the marathon (58). Furthermore, an analysis of 1.7 million marathons showed that both positive and negative pacing strategies are associated with reduced marathon performance, compared with an even-pacing strategy (59). These studies reveal a tendency for male recreational runners to adopt a positive split, which may hinder their performance. Although the reasons remain unclear, it may be speculated that the difference in pacing strategies originate from psychological differences between sexes (60).

Marathon performance is, indeed, a multifaceted phenomenon, regulated by a complex interaction of psychological and physiological factors. In an attempt to integrate both scientific disciplines and previous work, and building upon the central governor model (61), St Clair Gibson et al. (62) proposed the Integrative Governor Theory, whereby psychological and physiological drives compete and interact with each other, creating a dynamic system that regulates and controls observed behavior. In the case of a marathon, poor pacing may result in excessive speed that triggers a feedback loop whereby perturbations within the exercising muscle and other physiological systems result in an urge to slow (63), whereas psychological drives to continue may include the desire to complete the marathon within a target time (e.g., under 3 h). Allen et al. (64) used a very large dataset with ~10 million marathon performances to demonstrate the frequency of marathon finishing times increased close to popular target times (Fig. 2). Specifically, marathon runners appear to aim, or pace toward, a specific time (e.g., a sub 3-h marathon), and marathon finishing times immediately before such reference times (e.g., 2:58 or 2:59) are disproportionately more frequent than immediately after (e.g., 3:01 or 3:02). The data demonstrate the behavioral contributions to marathon performance, with goal attainment being an important driver of pacing regulation.

Training strategies and marathon performance.

Understanding marathon performance requires examining the characteristics of the training that athletes have undertaken in the weeks, months, or years, leading up to the event. However, systematically studying the causal relationship between training habits and performance is challenging. Elite athletes, for example, typically get involved in research studies for relatively short periods of time (e.g., for a few weeks or during a training camp) (12) and may be reluctant to participate in research studies that require a substantial change to their training schedule, fearing that such involvement could interfere with their preparation. As a result, much of the available evidence comes from studies reporting "best-practice" or "results-driven" approaches to training (8).

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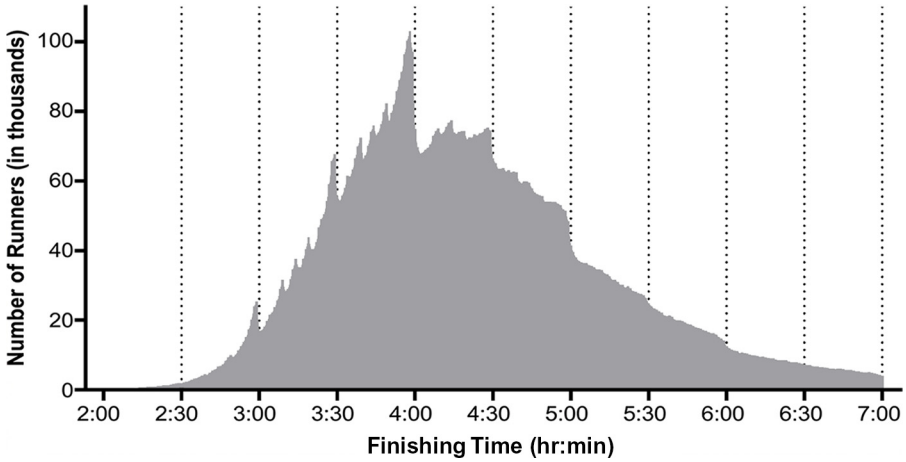

Figure 2. Natural experiment investigating the effect of reference times on marathon finishing. Results from ~10 million races demonstrated that athletes overcome the physiological drive to stop to achieve the goal of completing the race within a specific reference time. This is evidenced by the disproportionately high number of marathon finishing times recorded before common target times, e.g., 3:30 and 4:00. Redrawn with permission from data in Allen et al. (64).

Such "best-practice" studies are informative and provide unique insights into the training characteristics of, often, world-class distance runners, but have some methodological caveats. For example, it is unclear whether these athletes could have achieved a better performance had another training approach been taken. The ongoing debate on which training intensity distribution paradigm is best for endurance performance can illustrate this point (65, 66). Training intensity distribution describes the allocation of training resources, typically quantified as the proportion of training time spent across different intensity zones. Two competing paradigms dominate this narrative: the polarized versus the pyramidal. The proponents of the polarized paradigm suggest that athletes complete around 80% of their training at low intensity (i.e., in the moderate domain of exercise, typically below their lactate or ventilatory threshold), with the majority of the remaining ~20% allocated to train at high intensity (i.e., in the severe domain, above CS) and little training completed in between. The supporters of the pyramidal paradigm suggest that much of the training should be completed at low intensities alongside a higher proportion of training allocated to intensities in the heavy domain, between the lactate threshold and CS.

The effectiveness of different training intensity distribution approaches at increasing endurance performance has been studied either as a retrospective analysis of training patterns of elite athletes or in prospective studies in relatively short interventions (67–69). More recently, an analysis of the intensity distribution in >100,000 marathon runners across performance levels reported that a pyramidal approach was the most popular approach for all runners, and faster runners were more likely to adopt a pyramidal approach (70). Furthermore, the authors noted that markers of training volume, such as the number of training sessions, total distance covered, or distance covered at moderate intensity, strongly predicted subsequent marathon performance (70). These findings partially support evidence-based practices emphasizing the importance of high training volume for endurance athletes. However, they also underscore limitations in current approaches and demonstrate the need for further research, particularly regarding the optimal type and quantity of high-intensity training required to achieve peak marathon performance.

PRACTICAL APPLICATIONS, LIMITATIONS, AND FUTURE RESEARCH

Practical Applications

The findings from the natural experiments discussed earlier, derived from large datasets of training and performance data, could be of interest to participants, decision-makers, and other stakeholders involved in endurance running. The ability to estimate CS from training data and predict marathon performance or inform pacing has obvious applications to athletes and coaches. Indeed, the association between CS and endurance performance extends beyond marathon running (71), and training programs based on CS may be more effective than other approaches (72). Furthermore, in shorter running events, such as 5,000 and 10,000 m, where the intensity is likely to exceed CS at least for some sections of the race, modeling the finite amount of work (expressed in units of distance covered) that can be completed above CS, referred to as D′, has been shown to explain differences in performance between elite athletes (73). Similarly, continuous monitoring of the available W′, the cycling equivalent of D′, has been used to monitor performance during exercise and inform pacing strategies (74). The results from natural experiments discussed herein can help athletes optimize their chances of a world record or personal best (i.e., aim for races held close to sea level, in cold and dry weather, and at locations with low pollution), as well as help in the decision-making of race organizers assessing whether a race should go ahead in challenging weather conditions. Incidentally, the two attempts to break the symbolic 2-h barrier for the marathon incorporated some of the points discussed earlier: events took place close to sea level, in cold, dry weather, and runners were carefully paced by an electric car, which might minimize the detrimental effect of $PM_{2.5}$ (75).

Methodological Limitations

As participation in endurance and ultraendurance events grows and more performance variables are routinely measured, natural experiments using large datasets of training and physiological data, such as those described in this review, will become more common. Although these approaches address limitations of laboratory-based studies, they also introduce

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methodological challenges that researchers should consider. A frequent criticism is that variables derived from training or performance data may not conform to gold-standard laboratory procedures. For example, estimating CS from training data assumes that an athlete's recorded best efforts across multiple distances truly reflect maximal capacity (27). Similar CS values derived from habitual training and intentional maximal efforts have been reported (30), but this assumption might require further scrutiny, particularly for relatively less experienced recreational athletes. Furthermore, large training datasets are often complex, noisy, or incomplete because devices that capture running data may not be able to record other modes of training that influence endurance performance, such as strength training. Although these datasets can be large enough to allow meaningful patterns to emerge despite the noise, it does not eliminate issues around missing or incomplete information. Finally, it is worth highlighting that natural experiments are inherently descriptive and cannot determine causality in the observed relationships. Large datasets also carry a greater risk of producing spurious associations, particularly if many variables are analyzed simultaneously. Working with large datasets requires interdisciplinary expertise, and researchers must consider issues related to data privacy, consent, data ownership, and intellectual property.

Future Research

Future research should continue to assess whether metrics derived from natural experiments align with laboratory-based gold standards. Using CS as an example, further work could determine whether estimates obtained from training or performance data truly represent the physiological boundary between steady state and nonsteady state exercise, extending an approach already used in cycling (76). In addition, whether estimates of CS (or its equivalent in cycling, critical power) derived from training data in recreational runners (or cyclists) accurately capture the maximal metabolic steady state, as effectively as those derived from well-trained athletes, should be examined.

Research should also seek to further our understanding of the relationship between training inputs and performance outputs using large-scale datasets, including work incorporating machine learning or artificial intelligence (77–80). Collaboration between researchers and commercial platforms with access to large athlete populations could support prospective studies in which participants volunteer to be randomly allocated to different training approaches. Users, for example, may opt in to take part in a research study and then be randomly allocated to different training programs, with field- or laboratory-based testing used to assess the effectiveness of the intervention. Although this would not constitute a natural experiment, it would combine the advantages of large sample sizes with relatively controlled conditions and thus allow for a strong study design to assess competing hypotheses. Although we think laboratory studies will remain essential for validating and contextualizing findings from natural experiments, combining controlled trials with large-scale observational data may offer a more efficient use of resources, bringing together the precision of laboratory measurements and the scale of real-world datasets.

CONCLUSIONS

Experiments of nature and natural experiments are two types of passive experiments. The former investigates individuals with rare genetic or acquired conditions, whereas natural experiments focus on populations exposed to unusual environmental or behavioral stressors. In this paper, we argued that, despite its growing popularity, running a marathon remains an unusual physiological stressor. We presented natural experiments reporting on novel markers of endurance performance, and how environmental conditions (e.g., altitude, climate, or pollution) and behaviors (e.g., training before the marathon or pacing during the event) influence the observed outcome: marathon performance. These studies often rely on performance and physiological metrics that are analyzed retrospectively and compiled into large datasets. Although the results discussed here often align with findings from previous studies conducted on small cohorts under controlled laboratory conditions, the large sample sizes used in these studies can provide insights that could otherwise be undetectable in laboratory-controlled studies with smaller samples. Nonetheless, we recognize the value of laboratory testing and data collection under controlled conditions, which complement findings from large datasets. Therefore, future studies may explore a hybrid approach in which researchers conducting well-controlled laboratory experiments work with running platforms to design integrated hybrid studies that combine large sample sizes with laboratory-controlled interventions.

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DISCLOSURES

No conflicts of interest, financial or otherwise, are declared by the authors.

AUTHOR CONTRIBUTIONS

B.H. prepared figures; D.M.-P. drafted manuscript; E.M., B.S., and B.H. edited and revised manuscript; D.M.-P., E.M., B.S., and B.H. approved final version of manuscript.

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