Chapter 2
Physical Activity and Life History Theory

> …the fundamental theoretical issue faced by the social, behavioral, and medical sciences is how to build models of an ancient, but flexible, response system in a very novel environment.—Hillard Kaplan, 1997.

Life history theory (LHT) is a branch of evolutionary theory aimed at explaining differences in the age schedules of growth, reproduction, and mortality (Charnov 1993; Stearns 1992). LHT proposes that humans, like other species, face trade-offs in how to optimally allocate the limited resources of time and energy among growth, reproduction, and maintenance (i.e., immune function, survival, longevity). Optimal allocations between these demands are expected to depend on individual and ecological parameters that influence resource production, mortality, and other factors (Hill and Kaplan 1999). There are inherent trade-offs between somatic versus reproductive effort, current versus future reproduction, mating versus parental effort, and quantity versus quality of offspring. The theory posits that there have been long-term evolutionary pressures to balance energetic effort, and channel resources toward behaviors that maximize expected reproductive success across the life span. Life history strategies of energy allocation interact with the environment to fundamentally determine rates of growth, age of reproductive maturation, the pace of reproduction, reproductive senescence (particularly in humans), and life span.

Physical activity is particularly well suited for a life history perspective because it both influences and is influenced by life history parameters (such as age of reproductive maturation, survival, and longevity) and is central to both energy expenditure and (at least traditionally) energy acquisition. According to LHT, a trait, characteristic, or behavior is maintained over evolutionary time when its adaptive benefits outweigh its costs of time, risk, and energy invested. In this book, I contend that human physiology and psychology have been shaped by natural selection to maintain physical fitness and selectively engage in physical activity when the adaptive benefits outweigh the metabolic and opportunity costs. Conversely, when the benefits do not outweigh the costs (in terms of *reproductive* fitness, after all trade-offs), humans, like other animals, have evolved to conserve energy through behavioral and physiological shifts in energy allocation. This drive

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for optimization has been shaped throughout human evolution to flexibly respond to environmental and individual conditions that influence the costs and benefits of physical activity across the life span. Considering how the costs and benefits of physical activity have been shaped by natural selection offers a prime example of integrating proximate mechanisms within a functional framework.

Energetic Costs of Physical Activity

On the one hand, physical activity entails high energetic costs. In addition to the direct metabolic costs of performing physical activity, costs are also incurred to develop and maintain cardiovascular and muscular fitness in humans. Muscles consume about 40 % of a body's resting metabolic rate (Lieberman 2015). Muscle is much more energetically costly than adipose tissue, and the high costs of cardiovascular and muscular fitness in humans can be inferred from the significant decreases in fitness and strength in response to detraining (Booth and Lees 2007; Coyle et al. 1984; Houston et al. 1983). In a preliminary study, researchers saw decreased fat-free mass and increased abdominal fat after one week of decreasing the number of steps taken per day from ~10,000 to ~1400 steps by taking cabs and elevators rather than walking, cycling, or taking the stairs (Olsen et al. 2008). This result suggests that humans have a rapid shift in metabolism from devoting calories to maintain muscles instead being partitioned into fat when muscles are not being used, even for relatively short time periods. Exercise also leads to changes in metabolism that are protective against risks of obesity and type 2 diabetes in our modern environment (Bassuk and Manson 2005). However, the maintenance of this protective metabolic state also appears to entail significant costs, because it is lost remarkably quickly in the absence of physical activity. For example, improvements in insulin action have been shown to be reversed back to untrained levels in as little as 38 h without exercise in trained male athletes (Oshida et al. 1991), and insulin action is significantly reduced after just one day of sitting among healthy adults (Stephens et al. 2011).

A potential explanation for the rapid changes in metabolism in response to physical activity is that our metabolism has evolved to facultatively respond to changes in physical activity. Given that the majority of physical activity across human history was "obligatory" (in that, it was directly necessary to meet everyday needs), and the ability to consistently store food extra-somatically relatively recent, decreases in physical activity were likely associated with decreases in the availability of food in the environment. Those who were more efficient at storing fat during times of low activity would be better off during times when less food was available (Brown and Konner 1987).

On top of the direct metabolic costs, and costs of developing and maintaining strength and cardiovascular fitness, humans also face risks of injury in developing fitness, and opportunity costs when performing physical activity. That is, time and energy spent in physical activity or maintaining strength and physical fitness cannot be spent on other activities important for survival or reproductive success. Over the course of human history, physical activity was obligatory for producing the food, shelter, and protection necessary to survive and reproduce; this ensured that a greater weight was placed on allocating energy to physical activities to achieve these basic needs, relative to today. Opportunity costs also vary with age, sex, and individual condition. Trade-offs in allocating energy to physical activity versus reproduction are more acute at certain points in the life span. This is particularly true for females more than males, as women bear the heaviest burden of energy and time devoted to reproduction that is incompatible with physical activity. Differences in opportunity costs of physical activity according to sex and age are illustrated in an example from the Tsimane'.

The Tsimane' are an indigenous population in the Bolivian lowlands whose economy is primarily subsistence based. They engage in foraging and small-scale horticulture. Like many South American indigenous groups, the Tsimane' have adopted soccer as a principal form of recreational physical activity. While soccer is often played several times per week in any given village, there is large variation in how much time individual men and women devote to playing. The current theoretical framework would suggest that this variation can be explained, in part, by variation in the costs and benefits of participation. Among the Tsimane', girls can be found playing soccer often, but few women play. Among men, net caloric transfers of food to offspring provide a clear quantitative indicator of reproductive effort in the form of paternal investment. The peak net transfers from Tsimane' men to offspring occurs in their 30s, with an average net transfer of 1740 calories per day (Hooper et al. 2015). This peak occurs when their children are likely to be living at home, old enough to have substantial caloric needs, but young enough not to contribute much to the household resources. When men are younger, however, reproductive effort is concentrated much more on attracting mates and social partners, which need not trade-off as clearly against allocating energy to playing soccer. Many men do not marry until their mid-20s, and men recently married appear to maintain some level of mating effort, because they are more likely to have affairs, and many marriages break up in the first couple of years (Winking et al. 2007). Compared to younger men, older men may also be more prone to injury, or have more to lose if they do get injured because their bodies take longer to heal and they have more dependents relying on their food production.

Given these differential costs, I would predict that younger men (<30 years old) play soccer more frequently than older men, who must spend more energy producing food for their families and who may face higher risks of injury. A sample of 166 men from six Tsimane' villages supports this prediction (unpublished data from Benjamin Trumble, UC Santa Barbara, and Daniel Cummings, University of New Mexico). A t-test comparing men who are under 30, to those 30 and over showed that younger men played soccer significantly more days per week than older men $t(87) = 5.42$, $p < 0.001$. Younger men played an average of 3 days, with 75 % who reported playing soccer at least 3 days a week, with two men playing everyday of the week. Older men played just 2 days per week on average. Only 36 % of the older men played 3–5 days per week, and none over 5 days. The most frequent response, given by half of the older men, was only 1 day per week. While we know that older men produce more calories (Hooper et al. 2015), this analysis does not directly tell us whether there is a trade-off between time and energy spent playing soccer versus producing food. It could be that older men tend to buffer against unnecessary risks, or that their preferences for leisure time activities change over time, or that their fitness decreases, making it more difficult and less fun to compete with younger men. Each proximate explanation could serve the ultimate function of prioritizing physical activity that is consistent with primary reproductive benefits that change over time (i.e., mating versus parenting effort). Anecdotally, having seen the enthusiasm and joy expressed by all the men I have seen playing soccer; even in the face of losing to a rival community, heat, humidity, and exhaustion, I doubt that a lack of interest or enjoyment drives men to play less soccer. However, there is additional support for the hypothesis that time and energy spent producing food trades off against leisure time soccer playing. In a subsample of these men ($N = 50$), we also have data on how many hours per day they spend hunting (unpublished data from Paul Hooper, Emory University). In a regression model, the number of hours spent hunting per day negatively predicted the number of days per week spent playing soccer ($B = -2.24$, $p < 0.001$; controlling for both age and age squared). Therefore, holding the effect of age constant, averaging one more hour of hunting per day is associated with 2.24 fewer days of playing soccer per week.

Benefits of Physical Activity

Physical activity also has many benefits. As discussed previously, the decreased risk of many chronic and deadly diseases we see in our current environment are very important when considering the benefits of physical activity today. We will consider those in the final section on future directions, but the majority of this book focuses on those benefits hypothesized to influence reproductive fitness in ancestral environments. These hypothesized benefits include, but are not limited to: competing with rivals; attracting mates and social partners through displays of physical health and prowess; meeting the energetic demands of pregnancy, childbirth, and lactation; caring for children; producing food through foraging; processing food; protecting oneself and family from danger (including sexual predators); defending resources; migrating over long distances; building shelters; and collecting fuel for warmth and protection.

Summary and Applications

To summarize, there are substantial costs and risks associated with investing energy and time in physical activity that must be balanced with investing time and energy necessary to grow and maintain a healthy body, and reproduce successfully. In humans, reproducing successfully involves not only mating effort, but substantial parenting effort to increase the likelihood that offspring also survive and reproduce.

Beginning with the advent of agriculture, humans have been very successful at finding more efficient ways to extract resources. In even more recent human history, technological advances and globalization have led to an especially rapid and dramatic increase in the efficiency of resource extraction, distribution, manipulation, and consumption, such that little energetic expenditure is required to fulfill our basic biological goals. It is no coincidence that modern, Western environments have very few energetic demands in order to meet our survival and reproductive goals. Rather, they reflect our innate, evolved drive to decrease the energy required to meet these goals in order to conserve energy for growth, maintenance, and reproduction. The inborn conservatism of our evolved energy allocation systems discourages us from maintaining energy expenditures similar to Pleistocene ancestors in the absence of tangible evolutionary benefits. This innate drive to conserve energy has only recently been coupled with massive abundances of calorically dense, easy to acquire foods. Energy conserving behaviors and metabolic adaptations that increased the likelihood of survival and reproduction in environments with fewer and less predictable resources now lead to deleterious health problems and can even hinder reproduction. This has been termed a discordance or mismatch between adaptations and environments (Eaton et al. 1988, 2002; Lieberman 2013).

How can an understanding of the costs of physical activity as they relate to reproductive success inform efforts to increase physical activity and exercise in modern environments? One advantage of this approach is helping to differentiate between costs and benefits that are malleable versus those that are not, to design interventions to target those that are changeable, while working around those that are not. For example, the metabolic costs of performing physical activity cannot be changed by intervention techniques. They will change with experience performing physical activity, but an intervention cannot make running or other physical exertion somehow less costly, so people are more inclined to do it. Doing so would also make some people less drawn to it, or defeat the purpose, as people in our current environment seek exercises that help them expend as much energy as possible. Some people go to great lengths to change their workouts regularly to keep their bodies from acclimating to exercises and performing them more efficiently; our bodies want to expend less energy, so we have to stay one step ahead if we want to exert more.

However, an evolutionary framework can explicitly model and make predictions about factors that lead to individual differences in how people physiologically and psychologically respond to physical activity, training, and fitness that change the metabolic costs of activity at an individual level. For example, differences in condition brought about by inherited genetic variation (and potentially epigenetic changes), adaptations to developmental environments, prior physical fitness, burden to the immune system, access to resources (socioeconomic status) are all predicted to influence the individual costs of physical activity. Moreover, the metabolic and opportunity costs of physical activity change throughout the life span and are different in men and women (detailed in Part II). Considering the individual level costs can help to know when it may be more or less difficult for individuals to begin or continue exercise and may predict the extent to which conscious, cognitive processing is likely have a strong impact on behavior at a given point.

In contrast to the relatively rigid energetic costs of physical activity, the benefits are much more malleable because, while they all ultimately relate back to reproductive fitness and survival, they are partly defined by individual, ecological, and cultural factors. For example, there are traditional populations like the Tarahumara of northwestern Mexico that continue cultural traditions that include high levels of endurance running. Historically, the Tarahumara would hunt deer and antelope using persistence hunting, a form of hunting that requires endurance running and walking over long periods of time to exhaust and overheat prey (Lieberman 2014). The Tarahumara no longer practice this hunting technique, but the importance of endurance athleticism has remained a large part of their culture. They participate in annual *rarajipari* (for men) and *ariwete* (for women) games that in which teams of men kick and chase a small wooden ball for around 75 km (46.6 miles), and teams of women chase a hoop over shorter, but still extensive distances (≤40 km, ~25 miles). In this culture, being able to show physical prowess likely confers more benefits than in cultures where there is less of an emphasis on endurance athletic ability.

It is important to stress that critics of an evolutionary perspective have concerns that this approach is deterministic and presumes that behavior is determined by genes that were shaped by natural selection and play out regardless of environments or developmental experiences (e.g., Lickliter and Honeycutt 2003). In stark contrast, a LHT perspective transcends a false dichotomy of nature versus nurture. Instead, a LHT perspective predicts that the optimization system of energy allocation is what has evolved; it has been shaped to flexibly and adaptively respond to environmental and developmental cues regarding resource availability, how those resources are acquired, individual condition, and extrinsic mortality risks. This distinction is crucial for those interested in increasing health and wellness in current environments through increased physical activity, because it suggests that although there is a mismatch between the environment and adaptive behavioral and physiological responses, there is flexibility to shape the reaction norms, or trajectories of energy allocation, by manipulating the costs and benefits, and changing environmental conditions to require or at least favor higher levels of activity. A clear understanding of life history parameters and evolved energy allocation systems that influence physical activity in humans will also help us to find opportunities for increasing physical activity by reducing the costs or increasing the benefits, so the adaptive benefits outweigh the metabolic, maintenance, and opportunity costs involved. Toward that better understanding, we will begin this quest by examining the factors that are unique to human life history and the costs and benefits of physical activity from a phylogenetic and comparative perspective.

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