

Evolutionary imperatives and the good life

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Pondering the good life and how to lead it is probably a modern luxury (or perhaps a curse, people seem to differ on this issue). Our hunter-gatherer ancestors appear to have had plenty of spare time for reflection (ref), but it seems unlikely that this topic was a source of concern or contemplation for them. Nevertheless, even if the question is a uniquely modern one, there is reason to believe that a substantial part of the answer can be found in our distant past. Evolutionary pressures shaped our motivational system to guide us toward reproductive success, and thus consideration of our evolutionary imperatives might help us gain some traction on what it means to lead a good life.

On first reflection, an evolutionary guide to happiness would seem to be a pretty short pamphlet, or even just the simple advice to eat more and have more sex, and perhaps there is some truth to this. But the story is also much more complex. First, living the good life may well be a matter of meeting our evolutionary imperatives, but these imperatives are often at cross purposes with each other, and thus it requires a good deal of wisdom and self-knowledge to navigate between them. The clearest example of these cross purposes can be seen in our paramount goals of reproduction and survival. Despite their joint centrality, reproduction is actually the currency of evolution and survival is only of significance to the degree that it serves that goal. The resultant tension between reproduction and survival is evident throughout our motivational system, most notably in the competition between many of our short-term and long-term goals.

These challenges in meeting our competing evolutionary imperatives are then magnified by numerous other complexities, some ancient and some modern. On the ancient side, although our imperatives are universal, our strategies to achieve them are not. For many species there is only way way to get dinner or a mate, but for us the number of strategies we can adopt is limited only by our imagination. Thus, to understand how to achieve happiness it is also necessary to understand individual differences. This is not to say that the roads to

happiness are completely plastic, as they assuredly are not, but it is to say that people need to find a solution of best fit.

On the modern side, our highly technological world continues to develop new tricks to short-circuit our pursuit of happiness via what Robert Trivers calls *phenotypic indulgences*. Alcohol and other drugs, television, and even potato chips are all phenotypic indulgences, as they are designed to mimic ancient pleasures without actually delivering the outcomes that made those ancient activities adaptive (television may actually provide some of the benefits it is designed to mimic, but more on this issue later).

Lastly, and perhaps most importantly, lest all this discussion of meeting our evolutionary imperatives seem overly deterministic, it is important to keep in mind that we also evolved to be the most cognitively flexible species on the planet. Indeed, humans evolved to fill the cognitive niche that we created; we actively learn most of what we need to know to survive and thereby create our own life course. That doesn't mean that we can find happiness just about anywhere, as most of us cannot, but it does mean that we decide the importance of happiness in our life as well as the most fruitful way to pursue it. Understanding our evolved nature and the pressures exerted by our deep past can help guide us in this pursuit.

In the remainder of this chapter we consider our most important evolutionary imperatives, from reproduction and survival to learning, cooperation, and competition. We consider how to avoid being derailed by phenotypic indulgences, and conclude with a discussion of strategies of best fit. These strategies not only differ as a function of personality and abilities, but they also change in important ways across the life course.

Reproduction

Reproduction is the currency of evolution, but as Hamilton (19??) pointed out, our own reproduction is not mission critical so long as we enhance the reproductive success of our relatives. The central importance of reproduction does not mean, however, that humans or

any other animals have a desire to reproduce (e.g., Confer et al., 2010; Tooby & Cosmides, 1990). Indeed, it would have been a strange outcome if we had evolved a desire to have children, given that until very recently in our evolutionary history we would have had no idea how to achieve that desire. Thus, it should come as no surprise that evolution gave us a desire to have sex rather than a desire to reproduce, and then a tendency to feel nurturant to those children who came along as a consequence. One might argue that such a desire for sex in the absence of a desire for children is inefficient, and indeed it is. Humans have all sorts of sex that cannot lead to reproduction, but so long as they mix in enough of the reproductive sort of sexual activity, the costs of masturbation, oral and anal sex, and even sex with other species is likely to be low.

For this reason, *frequent sexual activity is likely to be a key to living the good life*. But frequent sexual activity alone is insufficient to successfully reproduce. The long period of dependency in human children dictates that parenthood is also critically important to reproduction, and indeed grandparenthood is important as well. For this reason, *raising and teaching our children and children are likely to be another key to living the good life*.

Although this may sound sexist, given the much greater obligatory investment required by women than men in raising their children, it seems likely that raising children (and probably also grandchildren) plays a larger role in female than male life satisfaction. Nevertheless, Hamilton's ideas of inclusive fitness clarify that it is in both men and women's best interest to facilitate the survival of their offspring and those of their close family, and thus providing for the next generation of our kin is likely to be an important source of happiness for everyone.

So far this recipe for happiness – have more sex and do a good job raising your children – probably seem inherently obvious to the most casual observer. But reproduction is more complicated than that, and so are its implications for life satisfaction. Probably the most

complicated aspect of reproduction is finding the right partner in the first place. Choosing a partner involves a fair degree of predicting the future, which is dicey at best. The difficulty of this problem is further exacerbated in pair-bonding species like our own, as partnership is a mutual decision, so it is not possible for all the males to mate with the most desirable females and vice versa. Due to the compromises necessitated by limited availability and mutual choice, it also follows that different people are likely to make different trade-offs when making these choices (given the importance of individual differences discussed above).

In response to these rather complex and fluid demands, the human motivational system appears to have evolved to maximize effectiveness in intra-sexual competition for the best and most individually suitable partner. In this manner, reproductive pressures ensure that happiness is driven by more than just sex and parenting, as it is also a product of those variables that increase our chances of pair bonding with the person with whom we most want to have sex and children. In other words, our motivational system is shaped by sexual selection; we want to be what the other sex is looking for.

What the other sex is looking for often feels like one of life's great mysteries, but the broad brushstrokes are not so mysterious at all. Men and women want many of the same things – e.g., kindness and generosity are near the top of everyone's list – and the differences in their desires have been also well documented (Buss ref). Setting aside the details, sexual selection pushes both men and women to strive for greater status than the people around them – not necessarily in all domains, but certainly in those domains in which people have the best prospects. This drive need not emerge in a conscious desire to put ourselves above others, but it should emerge in a desire for mastery and an aversion to inequality. Mastery is important because our unique skill set differentiates us from others and make us desirable as a mate. Inequality aversion is also fundamental, largely because it is difficult to attract a mate from the bottom.

In our modern world, both of these preferences can easily put us on a hedonic treadmill, whereby we try to attain wealth and status, continually hoping that a little more will make us happier than we are today. Unfortunately, the data suggest that wealth does little for us unless we have more than those around us do, suggesting that in fact it is status that we are really after. Two sets of findings illustrate this point nicely. With regard to status, research in macaques demonstrates that when monkeys rise to the top of the status hierarchy they increase the amount/availability of dopamine receptors in their brain. As a result of this increase, they no longer experience benefits from cocaine (a drug designed to hijack the dopamine system), and show no preference to self-administer cocaine over salt water (Morgan et al., 2002). Monkeys at the bottom of the status hierarchy, in contrast, become avid cocaine users.

Second, with regard to wealth, the data show that although it makes people happier when they become richer, once they get out of poverty the effects are not as strong as people think. And more importantly, if all of society rises in wealth at the same time, then increased wealth provides no increase in happiness at all. This effect can be seen by plotting life satisfaction against purchasing power over fifty-five years in the US (Figure 1a) and thirty years in the EU (Figure 1b). Thus, it seems that my flat screen TV, granite countertops, and convertible don't actually make me any happier unless I have them and you don't. This impact of relative wealth clearly implicates status, and with it, the role of sexual selection in life satisfaction.

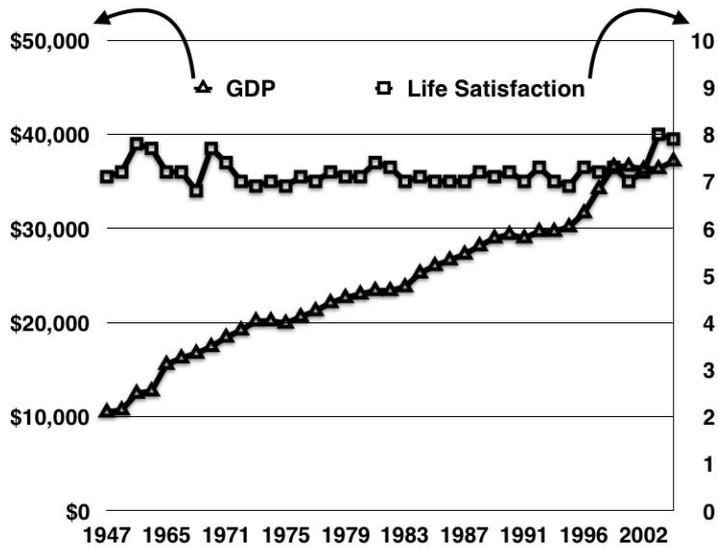


Figure 1a: Income and life satisfaction in the United States.

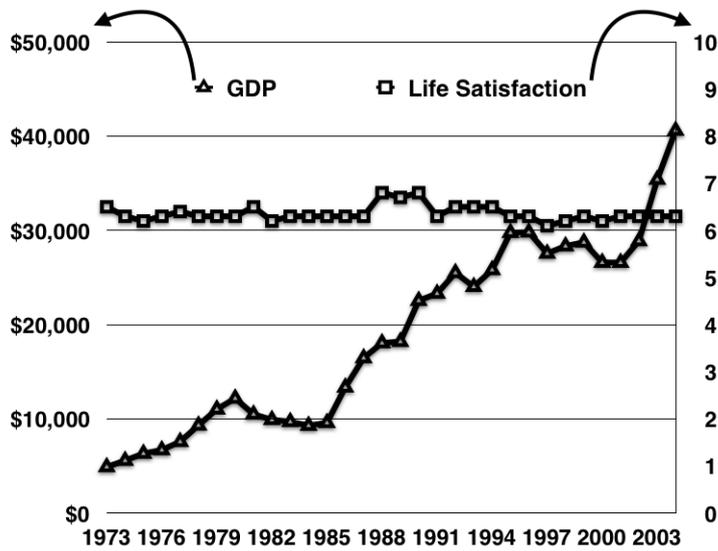


Figure 1b: Income and life satisfaction in the European Union.

Unfortunately, getting off this hedonic treadmill is no easy matter. Millions of years of sexual selection have ingrained status concerns into the deepest levels of our psyche, so turning them off or even ignoring them is impossible for most of us. But awareness of the issue probably helps, particularly since it can allow us to focus our attention on other aspects of our lives that have the potential to provide more lasting happiness. One partial solution is to spend money on fun activities rather than material goods – buy things to do rather than to have. Particularly when people move into the middle class, and go from buying necessities to luxuries, their experiential purchases make them a lot happier than their material ones (van Boven & Gilovich, 2003). The things we own lose their allure as soon as we reset our status goals, but the things we do become a part of us. Experiences give us the stories that we tell friends and family, our most important memories, and continue to provide satisfaction long after the experience has ended.

Survival

Survival goals are fundamental, and a great deal of our positive and negative emotions are tuned to our survival. We love fat, sugar, and salt because they were rare in our ancestral environment (ref), but critical for survival. We feel anxious and afraid when we walk through the woods at night, because we are far more likely to be prey than predator once darkness falls. We are highly attuned to the possibility that our friends or group members might reject us, and devastated when it happens, because expulsion from our group was a major life threat for our ancestors. And we feel comfort and security from home and hearth, as these were sources of protection from the elements and predators.

Nevertheless, despite their importance, survival goals are often trumped by reproduction goals, and we see this in numerous trade-offs. Perhaps the most notable example is senescence itself. We age and die in part because we spend precious resources in our efforts to reproduce rather than in tissue maintenance and repair (ref). Furthermore, a trait that helps

us reproduce when we're young will typically have a selective advantage, even if it kills us when we're old. Perhaps the most famous example of such an effect can be found in the $\epsilon 4$ allele of the ApoE gene, which is associated with an increased likelihood of developing Alzheimer's disease late in life (Corder et al. 1993). Somewhat ironically, this allele is also associated with better attention and memory early in life (Han et al. 2007), and thus probably facilitates status attainment and reproduction (and possible survival as well). As a consequence of the benefits it brings when we are young, the $\epsilon 4$ allele is widespread in our population. Because evolution often favors our tendency to sacrifice long-term survival in service of short-term reproduction goals, our motivational system shows substantial support for such trade-offs.

The clearest illustrations of such effects can be seen in dating and mating strategies themselves. Men take greater physical risks when in the presence of attractive women, and this rise in risk-taking is mediated by increases in testosterone (Ronay & von Hippel, 2010). Similar effects can be seen in many other animals. Because men are much more likely than women to leave behind no offspring at all, selection favors men who will risk their survival in service of the goal to reproduce. Physical risk taking also communicates reliable information about how robust and skilled a person is, which means that women use male risk taking as a sign of genetic quality. As a consequence, men are more likely than women to enjoy thrill seeking, and being a young male is one of the highest causes of mortality in industrialized countries (ref). Of course, women compete for men too, and the widespread use of dieting pills, tanning salons, and various other mating strategies show clear evidence of a willingness to sacrifice long-term health for short-term gains in attraction.

Cooperation and Competition

Our capacity for cooperation and social coordination was probably a key element that allowed our ancestors to survive the move from the trees. In the savannah our ancestors were

much more susceptible to predation, as lions, saber tooth tigers, and even hyenas are much faster and more powerful than bipedal hominins (Hart & Sussman, 2005). Although chimpanzees are probably best characterized as only occasional cooperators (Boesch, 1994; Gilby, 2006; Hare & Tomasello, 2004), reliable cooperation would have been essential for our ancestors to protect themselves from these predators, perhaps by collectively throwing stones (Bingham, 2000; Isaac, 1987; Calvin, 1982). Evidence for this possibility can be seen in changes to the bone structure of our hands as far back as *Ardipithecus* and *Australopithecines*, which enable better throwing than the hands of chimpanzees (Marzke, 1983; Napier, 1993; Young, 2003). Evidence for our fundamentally cooperative nature can also be seen and in the whites of our eyes, which in contrast to the brown eyes of other apes, display our gaze direction. The fact that we advertise the direction of our attention suggests that it is to our advantage to broadcast our intentions to other members of our group (Tomasello et al., 2007).

These anatomical data suggest that we evolved to cooperate with each other, and there are numerous changes in our minds and brains that support this conclusion. Our capacity to understand the different contents of the minds of others is much better developed than our chimpanzee cousins (Tomasello cite), and just as importantly humans seem to be unique in the desire to share the contents of our minds (Suddendorf, the Gap). Thus, it comes as no surprise that our motivational system is also tightly tuned to cooperation and group living.

Economists often seem surprised when people share resources with strangers that they could readily keep for themselves (Thaler cite), but this surprise only emerges from a misunderstanding of our evolutionary history. Because we evolved to cooperate with each other, we also evolved the capacity to readily detect free-riders, who reap the benefits of cooperation but do not themselves contribute (Barrett, Cosmides, Tooby, PNAS). Along with our cheater-detection system, we evolved a strong emotional response to free-riders, feeling

anger and righteous indignation when others take advantage of us (sanctioning institutions cite). These abilities and emotional responses ensure that others in our group cooperate with us, but they have also shaped the underlying cooperative motive itself. We don't like people who cooperate with us only to reciprocate, or to gain future cooperation in return. Rather, we like people who are friendly, kind, and generous without regard to consequences. In other words, we like people who enjoy cooperating for its own sake. And that, of course, means that other people like us for the same reasons, which would have given a substantial evolutionary advantage to our ancestors who genuinely enjoyed cooperating.

This is why we often share resources with strangers who will never be able to help us in return. Even though generous people occasionally get exploited, in the long run they win far more than they lose. Generous people are more popular than stingy or calculating people all over the world. When Hadza hunter-gatherers in Tanzania break camp and go off in different directions, the generous ones have lots of people who want to be with them while the stingy ones are at constant risk of being left alone (Apicella et al). And when the Aboriginal people of Northern Australia head off on their morning hunts, the generous people are always chosen as partners even if they're not the best hunters, while the stingy ones are often forgotten (ref).

The end result of these evolutionary pressures is that our motivational system is highly attuned to cooperation. We enjoy spending time with our friends and our kin, and we also attain great satisfaction from helping them. In the most recent World Values Survey (ref) of nearly one hundred countries, people around the world rated family as the single most important thing in their lives. But this altruistic satisfaction extends beyond close friends and kin to our entire community. Our communities are much larger now than the ones in which we originally evolved, but the psychological principles that link us to our community have the same effects that they have always had. As a consequence, our integration with our community is one of the keys to living the good life. Accumulation without sharing may be

important at some stages in life as people attempt to ascend the hierarchy, but to retain high status in a group it is necessary to form long-term and mutually beneficial relationships with others; that is, it is necessary to be regarded as a good and reliable friend. For this reason, life satisfaction is achieved by being a long-term resident in a stable set of social networks (i.e., embedded in one's community), and by supporting those community members who are in need.

Supporting community members in need is often accomplished through charity, but making a contribution to the community itself is probably the more important manifestation of this effect. We need to be of value to our community – our ancestors who were not judged to be of value were at risk of ostracism and hence death – and the most notable way to be of value is to produce more than you cost. This calculus probably lies in the backs of all of our minds, and drives us to be contributing members of society. When someone asks how you would like to be remembered (and hopefully eulogized) at your funeral, essentially they are asking what is the nature of your contribution to your community.

Learning

As we mentioned at the outset of this chapter, humans actively learn most of what we need to know to survive. We are born knowing very little and with a brain that is really only half-baked, but that would be too large to birth once fully cooked. As a consequence, we have an inordinately long period of development before we can become a viable and contributing member of our community. This period of development is consumed almost entirely by learning the means of survival used by our group. The importance of learning ensures that evolution linked learning tightly to our motivational system, and consistent with this possibility, humans all over the globe love to learn. Curiosity is one of our fundamental drives (ref), and the satisfaction associated with learning and mastering something new is universal (deci/ryan type cite).

Despite the widespread awareness of these principles, there are two important aspects of learning – and hence two important sources of life satisfaction – that are given relatively short shrift in the psychological literature: play and story-telling. Play is universal among mammals, most notably before they reach maturity, as it is a form of learning the rules and strategies of an adult life. Play helps juvenile males learn to compete for females (ref), it teaches strategies for eventually rising in the adult hierarchy (ref), and it helps juveniles learn strategies of predation and escape (ref). Because humans are unique in just how much they need to learn to survive and thrive, and how long that learning takes, the importance of play has extended beyond our childhood into our adult lives. As adults, play may enhance the quality of close relationships by fostering intimacy and improving conflict resolution skills (van Vleet & Feeney, 2015). For these reasons, play has a fundamental role in life satisfaction. This effect can be seen in the enjoyment of sport (and sport spectating) across the lifespan, and also in the importance of various games into late adulthood. In the absence of play, life is not nearly as worth living.

The importance of play is shared with all mammals, but story-telling appears to be unique to humans. Human learning has the enormous advantage over the learning of other animals in that our incredible communicative abilities ensure that we can incorporate the learning and accomplishments of others into our own understanding of the world. The oldest and most important form of this learning process is probably story telling (corballis?). Story telling is ubiquitous in all human cultures, and assuredly began as our hunter gatherer ancestors sat around in small groups at the end of the day and regaled each other with their experiences. Those who enjoyed telling stories and were talented at it would have gained stature in the group, as their presence in the group was thereby valued. Furthermore, everyone would have evolved a tendency to enjoy listening to stories, as that would provide a cost-free manner in which difficult and sometimes expensive lessons could be learned. Finally, story telling

would have connected community members to each other through shared emotional experiences, a sense of shared reality, and a common knowledge of how to approach the world.

For these reasons, telling and listening to stories are two of the great sources of human happiness and life satisfaction. When we feel that our stories are valued by others, and they share our understanding of the world, we feel validated and our importance to our group is assured. When our stories are dismissed or misunderstood, in contrast, we feel marginalized and unhappy. Perhaps this is one of the reasons for proliferation of urban legends, as research has shown that people exaggerate and invent components of the stories they tell largely to ensure that others share their emotional reactions (Heath cite). If I tell a story of being stuck forever on hold that fails to enrage the listener, then my story itself has failed its purpose, and the next time I tell it the details will have to be more outrageous to ensure my audience responds as I did.

Personality and Development

As we suggested at the outset of this chapter, there is more than one way to be a success as a human and hence more than one route to happiness as well. If I'm big and strong I might attract a mate through sport or other physical competition, but if I'm small and weak I might be better off using my humor or kindness. Such individuals might also be suited to different types of careers. In many animals there is only one route to success, but fortunately humans have many options open to them. As a consequence, people naturally tend to choose a strategy of best fit by maximizing their phenotypic advantages. That is, people pursue activities that rely on their strengths and that minimize the impact of their weaknesses. Because our motivational system is attuned to success and the degree to which our group values us, this means that different activities will make different people happy, largely depending on their abilities compared to others in different domains. If I am a better artist

than most other people but a worse athlete, I will probably find greater satisfaction from art than from sport.

These individual differences, in turn, also change over the course of our lifespan. As a child it is very difficult to contribute to one's group, and hence children gain most of their sense of happiness and satisfaction from their activities with one another and from acceptance and support by their parents. Because their unique features are more likely to be noticed by others than their common ones (McGuire cites), their sense of self nevertheless becomes most tightly attuned to the unique ways that they can differentiate themselves positively from their group. That is, children start to develop their unique set of talents that will make them most productive when they reach adulthood.

Once we attain adulthood, our contribution to the community becomes important, and we start to rely on those skills that we learned in an effort to rise up the status hierarchy and be valued by other members of our group. These skills and activities are relatively stable in most people throughout their young and middle adulthood, but begin to show reliable changes in late life. At that point, physical skills often deteriorate. Older adults tend to have a larger body of knowledge, which made them valuable in our ancestral past and offset their deteriorating physical skills. Unfortunately, in our modern and rapidly changing world that knowledge can become obsolete as well. But the evolutionary pressures that push us to contribute to our group don't change just because we have gotten older, and thus many older adults strive to find ways to continue to make a positive impact on their community. This is one of the reasons why approximately one third of people who are recently retired have a great deal of difficulty adjusting to their new life, even if they were looking forward to it previously.

As a consequence of these processes, the sources of our life satisfaction also change as we enter late adulthood. Because we evolved to feel happy when we contribute to our

community, we also evolved to seek different sources of life satisfaction as the nature of those contributions changes over the lifespan. Issues of legacy and care for others become increasingly important among older adults, as these are often their greatest opportunities to remain connected and helpful to others.

Pitfalls of a Modern World

Pondering the good life may be a uniquely modern pastime, but the ways that we achieve it are by following the ancient strategies that made our ancestors successful. Sex and eating, parenthood and play, mastery and storytelling, friendship and kin, hearth and home, community and contribution – these are the keys to success in our past and they remain the keys to our happiness today. Nonetheless, our modern world provides many new opportunities for happiness, and it is not at all clear when the modern version is just as good as the original.

For example, movies and television have replaced some aspects of story-telling, and they remain some of the most fun things that we do (kahneman cite). But story telling is much more than just relating a series of events, and movies and television don't connect people to each other in the same way that conversations do (until we talk about them later). To some degree, movies and television are thus a phenotypic indulgence (like potato chips), and so it is no surprise that people rarely cite television programs as an important source of life satisfaction. Books are more likely to have an important and lasting effect on us than TV (ref?), which suggests that a critical part of storytelling is the imaginative and generative processes taking place in our minds when someone tells a tale that we cannot physically experience. But even books are typically less memorable and important than the stories we tell and are told, because reading is typically done alone.

Other aspects of our modern world that are designed to mimic important ancestral experiences provide much thinner gruel and leave us a lot less satisfied. Drugs and alcohol

are probably the most notable example of such phenotypic indulgences, as they go straight to the brain regions responsible for pleasure without providing the physical or experiential basis from which that pleasure was meant to emanate. After drugs and alcohol, junk food comes a close second, as the sugar, fat, and salt that our ancestors desperately sought in the past are overabundant today. One need only look at the dentition of Neanderthals – who never owned a toothbrush but never got a cavity – to see the health consequences of our modern agricultural diet. Sadly, our struggle is now against what was once a healthy goal to eat as much sugar, fat, and salt as possible.

The costs that we pay when we have too much of a good thing bring us to the final lesson that our evolutionary history can teach us about how to live a happy and meaningful life. Long-term relationships were our ancestors' best recipe for raising successful offspring, and as a result we find long-term relationships particularly rewarding. When people partner with the right person, they have their best shot at a lasting increase in happiness. But evolution also gave us a preference for novel partners, as both men and women gain reproductive benefits when they put their genetic eggs in more than one basket. The problem is that novel partners were relatively rare in our ancestral environment, as we spent our entire lives in the same small group of people. But just like fat, salt, and sugar, we now live in a world in which there is an unending supply of novel potential partners, who serve as a constant temptation for us to abandon our current relationship to try out a new and more exciting one. Of course, the new relationship will soon become old, and hence the allure of novelty is fleeting by definition, and eventually unsatisfying. Nevertheless, that fact doesn't prevent many of us from being serial monogamists now, and it didn't prevent our ancestors from adopting a similar mating strategy back then.

Most people are better at avoiding temptation than resisting it, and sure enough people who escape the lure of novelty usually achieve this goal by not exposing themselves to it.

Marriages last longer in rural areas than in cities, and much longer still if you're a nobody than if you're a famous actor or rock star. And this fact brings us back to the German folk saying about the inevitable disappointment we experience when we achieve our goals.

Universal adoration and fame are some of the most common dreams of people all over the world, but you need only reflect on the turbulent lives and repeated divorces of celebrities to realize how much happier you are being unknown.

Conclusions

Why did evolution play this dirty trick on us—giving us dreams of achievement that will provide lifelong happiness but then failing to deliver the goods when we achieve our goals? The answer to this question lies in the fact that evolution doesn't care if we're happy so long as we're reproductively successful. Happiness is a tool that evolution uses to incentivize us to do what is in our genes' best interests. If we were capable of experiencing lasting happiness, evolution would lose one of its best incentives. Our inability to achieve lasting happiness pushed our ancestors to achieve further goals, with the end result that they left more offspring in the next generation. We see a similar pattern today when we examine the motivational effects of happiness over time. Really happy people are rarely high achievers, because they simply do not need to be. Research on the relationship between prior happiness and future earnings (Oishi, Deiner, & Lucas, 20XX) reveals that moderately happy people go on to earn the more money than very happy people. Some joy is clearly good for success in life, but too much happiness is a motivational disaster.

References

- Bingham, P. M. (2000). Human evolution and human history: A complete theory. *Evolutionary Anthropology*, 9, 248-257.
- Boesch, C. (1994). Cooperative hunting in wild chimpanzees. *Animal Behaviour*, 48, 653-667.

Calvin, W. H. (1982). Did throwing stones shape hominid brain evolution? *Ethology and Sociobiology*, 3, 115–124.

Confer, J. C., Easton, J. A., Fleischman, D. S., Goetz, C. D., Lewis, D. M., Perilloux, C., & Buss, D. M. (2010). Evolutionary psychology: Controversies, questions, prospects, and limitations. *American Psychologist*, 65, 110-126.

Corder, E. H., Saunders, A. M., Strittmatter, W. J., Schmechel, D. E., Gaskell, P. C., Small, G. W., Roses, A. D., Haines, J. L. & Pericak-Vance, M. A. (1993) Gene dose of apolipoprotein E type 4 allele and the risk of Alzheimer's disease in late onset families. *Science*, 261, 921–23.

Gilby, I. C. (2006). Meat sharing among the Gombe chimpanzees: Harassment and reciprocal exchange. *Animal Behaviour*, 71, 953-963.

Han, S. D., Drake, A. I., Cessante, L. M., Jak, A. J., Houston, W. S., Delis, D. C., Filoteo, J. V. & Bondi, M. W. (2007) Apolipoprotein E and traumatic brain injury in a military population: Evidence of a neuropsychological compensatory mechanism? *Journal of Neurology, Neurosurgery, and Psychiatry*, 78, 1103–08.

Hare, B., & Tomasello, M. (2004). Chimpanzees are more skilful in competitive than in cooperative cognitive tasks. *Animal Behaviour*, 68, 571-581.

Hart, D., & Sussman, R. W. (2005). *Man the hunted: Primates, predators, and human evolution*. Boulder: Westview Press.

Isaac, B. (1987). Throwing and human evolution. *African Archaeological Review*, 5, 3-17.

Marzke, M. W. (1983). Joint functions and grips of the Australopithecus afarensis hand, with special reference to the region of the capitate. *Journal of Human Evolution*, 12, 197-211.

Morgan, D., Grant, K. A., Gage, H. D., Mach, R. H., Kaplan, J. R., Prioleau, O., Nader, S. H., Buchheimer, N., Ehrenkauffer, R. L. & Nader, M. A. (2002). Social dominance in

monkeys: Dopamine D2 receptors and cocaine self-administration. *Nature Neuroscience*, 5, 169–74.

Napier, J.R., (1993). *Hands*. Princeton, NJ: Princeton University Press.

Tomasello, M., Hare, B., Lehmann, H., & Call, J. (2007). Reliance on head versus eyes in the gaze following of great apes and human infants: The cooperative eye hypothesis. *Journal of Human Evolution*, 52, 314-320.

Tooby, J., & Cosmides, L. (1990). The past explains the present: Emotional adaptations and the structure of ancestral environments. *Ethology and Sociobiology*, 11, 375-424.

van Boven & Gilovich (2003). To do or to have? That is the question. *Journal of Personality and Social Psychology*, 85, 1193-1302.

Van Vleet, M., & Feeney, B. C. (2015). Young at heart: A perspective for advancing research on play in adulthood. *Perspectives on Psychological Science*, 10, 639–645.

Young, R. W. (2003). Evolution of the human hand: The role of throwing and clubbing. *Journal of Anatomy*, 202, 165–174.