

**The Evolutionary Foundations of Hierarchy:
Status, Dominance, Prestige, and Leadership**

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“Who can say for sure that the deprivation which afflicts him with hunger is more painful than the deprivation which afflicts him with envy of his neighbor’s new car” – JK Galbraith

The imperial city of Rome was the largest urban area in the world of its time. Despite being a democracy, Rome had an elaborate system of ranks and social standings visible to all. The Roman dress, the toga, was a status symbol par excellence; only free Roman citizens could wear it. Foreigners, slaves and even exiled citizens could not wear it in public, and it was taboo for Roman citizens to be seen in public without wearing one. Social status within the citizen class was further demarked by different kinds of togas. On formal occasions most Roman men and ordinary members of the Senate wore plain white toga virilis, whereas politicians campaigning for public office wore the conspicuously ultra-white, bleached toga candida. The white toga praetexta had a broad purple stripe on its border, and only priests and magistrates could wear it. Finally, the toga picta, a brightly coloured and richly embroidered garment, could only be worn by military commanders on their triumphs through the streets of Rome and by the consuls and emperors on special occasions like the Gladiator Games (Baker, 2010).

Rome was not unique in emphasis of status. All human societies, large or small, wealthy or poor, industrialized or subsistence based, have status hierarchies. The anthropologist Donald Brown (1991) has documented social status as universal across human cultures, and hierarchy is conceptualized as one of the key, universal dimensions of human social relationships in Fiske’s (1992) Relational Model Theory. Even foraging societies that might appear egalitarian at first blush are characterized by status hierarchies and, like the Romans, individuals at higher places in status hierarchies enjoy special benefits. For example, adult males of the Ache, an indigenous foraging people in Paraguay, invest large amounts of time and energy into acquiring meat. In a sense, hunting is their job, and meat is their income. The tangible fruits of one individual’s labors, though, cannot be

stored long-term in a manner that could allow the accumulation of capital and the subsequent status increases that real estate moguls, wall street executives, and heads of state enjoy. Instead, meat is shared with other members of the group in a relatively egalitarian manner. This egalitarianism in terms of tangible resources does not prevent the accumulation of status based on hunting performance, though; the best hunters in the band accumulate prestige, which allows them to have more extramarital affairs and sire more children than the average hunter (Hill & Kaplan, 1988). Similar associations between hunting skills and reproductive success have been reported among other hunter-gather societies such as the Ache, Hadza, !Kung, and Tsimane (Von Rueden, 2014).

In addition to being common across human cultures, status hierarchies are prevalent in non-humans social species as well (Ellis, 1995). A widely cited example is the pecking order in chickens. If a group of chickens is placed together for the first time, they will all initially peck each other in competition over food. Before long, though, a simple linear hierarchy emerges within the group where every hen knows its place: A pecks B, B pecks C, and A, B, and C all peck D, and so on, and the pecking order determines which hens gets preferential access to food. Hierarchy also determines access to females in various primate species (to which humans are closely linked). There are positive associations between male rank and reproductive success among chimpanzees, bonobos, gorillas and rhesus macaques, although the strength of the association varies depending upon socio-ecological conditions such as (a) resource predictability, (b) the ability to monopolize resources and (c) form levelling coalitions against dominants (Boehm, 1999; Ellis, 1995).

Given the ubiquitous nature of status hierarchies across human and non-human groups, and the fitness-relevant consequences of placement in status hierarchies (e.g., access to food and mates), it is likely that natural selection would have favored psychological mechanisms that are specialized for navigating status hierarchies. This chapter explores these mechanisms in several ways. First, we define the relevant concepts. Then we discuss the selection pressures that might have favored the evolution of a universal status striving tendency. We do this partially through the logic of a simple

game theoretical model. Third, we review some of the proximate mechanisms -- including behavioral, morphological, hormonal, and affective systems -- through which individuals are able to assess their relative status and likelihood of winning a status challenge, make status gains, and manage status losses, whereby we pay attention to sex differences in status striving. Finally, we investigate the emergence of one specific high-status position in human groups, leadership.

Definitions

Following Cummins (2005), we define *status* as an individual's standing in the social hierarchy which determines priority access to resources in competitive situations. We further draw a distinction between status hierarchies based on *dominance* versus *prestige* (Henrich & Gil-White, 2001; note that social psychologists Magee and Galinsky [2008] use the terms *power* versus *status*, respectively, to refer to these concepts). In dominance hierarchies -- which are common among nonhuman primates -- individuals achieve priority access to resources through threat, intimidation and displays of force. Prestige, in contrast, is freely deferred status granted to individuals because they help other individuals achieve their goals. In return, prestigious individuals (e.g., individuals with valued skills or knowledge) receive priority access to resources (Hill & Kaplan, 1988). Power, a concept recently explored by social psychologists, refers to the ability to influence others' outcomes by virtue of someone's control over resources, often based on position in the hierarchy (Keltner, Gruenfeld, & Anderson, 2003; Magee & Galinsky, 2008). Finally, it is useful to distinguish between *status* hierarchies and *decision-making* hierarchies, although these are often times conflated particularly in humans (Van Vugt, 2006). *Leadership* refers to a special position in the decision-making hierarchy where individuals exercise disproportionate influence on group decision-making, and can gain priority access to resources in return (Price & Van Vugt, 2014; Van Vugt, 2006).

An Evolutionary Psychology Perspective on Status

Given that a) status hierarchies are ubiquitous across observed human societies, both modern and historical, b) status hierarchies are observed in non-human primates, as well as other

animals, and c) an individual's position in status hierarchies has consequences for access to sexual partners and other fitness-relevant resources, humans likely possess evolved psychological mechanisms that for status-striving and navigating status hierarchies. These mechanisms a) motivate individuals to advance their positions in status hierarchies (*status improvement*), b) convert advantageous status positions into fitness benefits (*status capitalization*), c) assess and monitor others' positions in status hierarchies (*status assessment*) and d) manage and cope with changes in status positions in social hierarchies, both gains and losses (*status management*). These mechanisms are instantiated as coordinated interactions between hormonal, cognitive, emotional, and behavioral systems and they need not be consciously motivated.

An evolutionary psychology approach assumes that the psychological systems of status take the shape of stimulus-response mechanisms that can be seen as conditional ("if-then") decision rules that produce behaviors that were, on average, adaptive in the ancestral environment (Gigerenzer & Goldstein, 1996; Tooby & Cosmides, 2005). A conditional rule such as: "Only challenge an individual's status if the likely benefits outweigh the costs" enables individuals to achieve better pay-offs than a decision rule to "challenge anyone's status." Multiple selection mechanisms might have shaped this type of modular status psychology. Some evolutionary theories stress individual competition as the basis for status differences, viewing hierarchy as the resultant of individuals pursuing their own interests. Evolutionary biologist George Williams (1966) remarked: "The dominance-subordination hierarchy...is not a functional organization. It is the statistical consequence of a compromise made by each individual in its competition for food, mates, and other resources. Each compromise is adaptive but not the statistical summation" (p. 218). Other evolutionary theorists stress the functionality of status differences for both individuals and groups. One may be better off as a low status member in a group with a stable hierarchy than a high status member in an unstable group (Caporael, 1997; Ronay et al., 2012). Accordingly, social hierarchies in humans may be the product of selection operating at multiple levels (e.g., group and individual; see Wilson, Van Vugt & O'Gorman, 2008; compare with Pinker, this volume).

Game Theory and Status

Status striving can be conceptualized as a social strategy that has been selected for by virtue of its role in fostering reproductive success. This can be illustrated by applying insights from evolutionary game theory (Maynard Smith, 1982), which models social interactions as games in which strategies compete with each other in a Darwinian fashion. Evolutionary game theory is like economic game theory, except that the agents are genes, which embody strategies that are pitted against alternative strategies. Strategies, and the genes that lead to their development within individual organisms, spread through a population by virtue of the superior decision rules they produce in fitness relevant situations, whereas inferior strategies are culled from the population.

We can model status interactions as different social strategies in a game of Chicken (Figure 1), which parallels the well-known Hawk-Dove game in evolutionary biology. The name “chicken” stems from a game in which two car drivers drive towards each other on a collision course. One must swerve or both may die in a crash; yet if one driver swerves and the other does not, the one who swerved is called the chicken (coward). The principle of the game is therefore that while each player prefers not to yield to the other, the worst possible outcome occurs when both players do not yield. Status interactions have the feature of a Chicken game in which one can assume that players have two available strategies, either to challenge for status (Dare) or avoid a status confrontation (Yield) -- these are akin to the hawk and dove strategies, respectively. A challenger always wins against an avoider, and can therefore gain status. Pursuing a Dare strategy is thus effective when there are lots of Yield types around who will accept your status. But as Darers become more common in a population -- because they convert resources gained in status competitions into fitness -- interactions between them will increase. These interactions result in negative payoffs for both parties (Figure 1). In populations with many Darers, individuals who bow out of intense competition can thrive. The Yielders might have to surrender resources to the Darers, but they avoid costly battles, and their interactions with other Yielders are fruitful. Hence, there is a counter-surge of Yelder types in the population. Under certain conditions, the population will reach a mixed equilibrium of Dare and Yield

strategies over time, at the point at which each strategy enjoys similar expected reproductive success. This is a classic example of frequency-dependent selection (Buss, 2009; Maynard-Smith, 1982).

Animal research supports the principles of this status game. Consider orangutans, where males differ greatly in size. The flanged males are physically large, and they attract females to their territories by making loud vocal calls. The unflanged males are weaker and smaller, and they do not hold a territory themselves. Their strategy is to avoid the big males, and to wait for the opportunity to mate with an unguarded female (Harrison & Chivers, 2007). This explains why these two strategies continue to co-exist in the male orangutan populations at particular frequencies. Similar alternative mating strategies, reflecting the dare and yield tactics, have been observed in cuttlefish, salmon, and beetles (Hunt & Simmons, 2001).

The Dare-Yield combinations are referred to as the game equilibria. Once interactions settle into an equilibrium state, they are likely to remain there because neither player obtains a better outcome by switching to a different strategy (this is called an 'evolutionary stable strategy' (ESS) or in economics and political science, a Nash equilibrium). This game thus selects for adaptations that exploit equilibrium state of D-Y interactions, potentially giving rise to a stable status hierarchy. The implications of the model for the formation of status hierarchies are multifold. First, the benefit of Dare is higher in an interaction with a Yielder and a Yielder always defers to a Darer. Second, it is better to Yield in interacting with a Darer (especially if the darer is likely to win the status competition). Third, the combined pay-offs of the D-Y interaction are better than for pairs of either D- or Y-types. Thus, groups composed of Darers and Yielders tend to have better gross payoffs than homogenous groups. In contexts of intergroup competition, this dynamic might favor groups with a mixed assortment of status strategies (for empirical evidence, see Ronay et al., 2012).

The Chicken game analysis offers a potentially valuable lens through which to think about status adaptations and our evolved psychology of status. First, it shows why humans should strive to improve their status, as this determines their differential access to resources (Frank, 1985). Second it

shows how groups can arrive at relatively stable status hierarchies (the game equilibria) instead of facing constant challenges for status. Third, it provides an analytical framework for answering questions that parallel some of the foundational issues within social and personality psychology – for instance, how phenotypic qualities of the individual (a la the “person) interact with the situations they find themselves in (cf. Kenrick & Funder, 1988; Lewin, 1946; Reis, 2008)? Individuals lacking the phenotypic qualities to challenge for status, such as those lacking in physical strength or valuable skills, should avoid the costs of status competition.

Fourth, these status strategies should be conditional. Individuals predisposed to challenge for status should switch to a Yield strategy in situations in which they are likely to come up against a more formidable opponent or an opponent that is more committed to compete. The latter explains the home advantage effect documented in studies of animal behavior in which individuals that own territories are likely to fight harder than the ones invading a territory. Fifth, depending upon relative pay-offs of low or high status, we expect status confrontations to vary in intensity. The relative benefits of a challenge, for instance, may be greater for men than for women, which could explain the commonly observed sex differences in status striving, risk taking and dominance (Hogan, 2006). Finally, the game offers insight into status challenges between groups, where one group lacking the qualities to compete (e.g., through lack in numbers or resources) may yield to another group and a stable between group hierarchy might emerge. The game analysis forms the foundation of social psychological theories of intergroup processes, explaining why individuals identify more with high status groups, and are motivated to make costs to improve their group standing (Tajfel & Turner, 2004).

This parsimonious game is naturally limited in a number of ways. It is agnostic regarding the nature of the costs inflicted in status challenges (e.g., physical or psychological costs), and it says nothing regarding the proximate mechanisms underlying status interactions -- how do individuals signal their phenotypic qualities to each other and what qualities do they signal? Although we assume that such signals have evolved to be honest, in actual status interactions signals may be

faked (e.g., lowering your voice pitch during a job talk). Finally, the game is agnostic about whether status battles are based on dominance, prestige, or a combination (e.g., scientists and ultimate fighters compete in very different ways for status).

Status Systems

Status and Hormones

Testosterone. Human and non-human animal studies suggest that hormones are one of the proximate mechanisms that facilitate the emergence, development, and maintenance of status hierarchies in groups. Levels of the androgen testosterone (T) relate to individuals' relative status in both human and non-human samples (Archer, 1996; Ellis, 1995; Sapolsky, 1990), and not due only because shared relationships with third variables such as age, sex, or size. After intra-sexual competition – competition within one sex for access to mates -- victors on average experience an increase in testosterone whereas losers experience a decrease in testosterone. This pattern has been observed in direct physical competitions, in non-physical competitions, in experimental competitions within the lab, and in natural competitions (e.g., wrestling; Gladue, Boechler, & McCaul, 1989; Mazur & Booth, 1998; Mazur, Booth, & Dabbs, 1992). Changes in testosterone also occur vicariously and as a result of status competitions among groups. During the final match of the 1994 FIFA World Cup between Brazil and Italy, researchers found an increase in testosterone levels among fans of the winning team and a decrease in testosterone levels among fans of the losing team (Bernhardt, Dabbs, Fielden, & Lutter, 1998). The relationship between status and testosterone also appears to be bidirectional, with changes in testosterone producing a change in position in the social hierarchy. When biologists administered testosterone to low ranking cows, for example, the cows' hierarchical positions increased; when testosterone was subsequently withdrawn, the cows' position dropped (Bouissou, 1978).

Yet it is not quite clear how these testosterone changes convert into reproductive outcomes. One possibility is that increasing T motivates individuals to adopt a dare strategy (cf. Archer, 1996). Evidence linking testosterone and dominant/aggressive behaviors has been found among men in

highly intrasexually competitive prison populations and in non-prison populations (Mazur & Booth, 1998). Testosterone might also stimulate individuals to engage in prestige battles. After being administered a small dose of testosterone, participants gave more money in an economic game, compared to a control group receiving a placebo when giving money produced reputation benefits (Eisenegger et al., 2010).

The nature of the relationship between testosterone and status can be illuminated by considering the energetic tradeoffs that testosterone facilitates. Ellison (2003; Ellison & Ellison, 2009), for example, conceptualizes testosterone as regulating male reproductive effort. Higher testosterone levels during development produce “masculine” traits such as a more prominent brow ridge and larger jaw, a deeper pitched voice, and greater muscle mass. Such masculine traits are useful in dominance competitions, including physical combat, as well as in prestige contests, including mediation in conflicts (Von Rueden, 2014). Increases in testosterone following competition victories can be interpreted as general increases in energy allocating to mating effort, then. If testosterone also serves as an input into some of the psychological mechanisms governing mating displays, then these increases in testosterone following success in intra-sexual competitions can lead individuals to convert their victories into reproductive opportunities (*status capitalization*).

Engaging in status competition can be costly, both in terms of the energetics associated with testosterone production (e.g., Muehlenbein & Bribiescas, 2005) and in terms of the direct challenges from conspecifics that increased testosterone leads to, fighting other challengers. Given these costs, individuals who pursue an avoid strategy should be more wary of being placed in a high status position in which they are frequently challenged. Josephs et al. (2006) provide some support for this hypothesis. After rigging a competition, they observe that lower testosterone individuals placed into a high status position (i.e., victors in a competition) and high testosterone individuals placed into a low status position (i.e., losers in a competition) show patterns of relatively high arousal, with greater heart rate, and worse performance on tests of cognitive performance. In addition, those individuals who experienced increases in testosterone after losing the competition wanted to compete again

with the same individual; those individuals who decreased testosterone after losing wanted to avoid another confrontation (Mehta & Josephs, 2006).

Cortisol and serotonin. Testosterone is not the only hormone that regulates positions in status hierarchies. Indeed, cortisol also fluctuates in response to situations or events that might alter positions in status hierarchies. Those situations that lead to transient increases in cortisol are often subjectively experienced as “stressful.” Like testosterone, cortisol functions to regulate the allocation of energy to different physiological systems. Unlike testosterone, however, changes in cortisol function to supply the organism with extra bursts of energy by extracting glucose from physiological reserves that are lower priority in emergency situations (Ellison & Ellison, 2009). Adults and children of low socio-economic status typically show higher cortisol levels than those of higher socio-economic status, suggesting more frequent exposure to daily stressors (Kapuku, Treiber, & Davis, 2002; Marmot, 2004). Among married couples, the perception of the dominance of one’s spouse correlates with blood pressure reactivity during marital interactions (Brown, Smith, & Benjamin, 1998). Low-ranked managers have higher baseline levels of cortisol than higher ranked managers in organizations (Sherman et al., 2012). Although the causal direction in these relationships is yet unclear, it is consistent with Sapolsky’s (1990) baboon studies showing that lowly ranked baboons experience continuous elevated levels of cortisol. An interpretation of this effect is that cortisol buffers against a low status position with an associated lack of resources (see Figure 1) by making more energy reserves available.

Finally, high status has been linked to elevated levels of serotonin, a neurotransmitter, primarily found in the central nervous system, which is thought to be related to feelings of happiness and well-being. Primate studies have found that as individuals move up the social hierarchy of their group, their serotonin levels increase (Sapolsky, 1990). Experiments with vervet monkeys show that males with high social rank had almost twice as much serotonin in their blood as did the low-ranking monkeys (Raleigh, McGuire, Brammer, & Yuwiler, 1984). A causal link between serotonin and status was established when scientists administered citalopram (a serotonin drug) to 10 healthy volunteers.

While taking the drug, these volunteers were rated as significantly more dominant by observers, and they also increased their eye contact when interacting with strangers compared to a placebo group (Tse & Bond, 2002). Not surprising, drugs to fight depression and anxiety in humans (e.g., Prozac) work by increasing serotonin levels in the brain. Serotonin may well be an internal cue of one's status position in a group.

Status and Physique

To the extent that position in status hierarchies and competitions for status (and, ultimately, mates) favor physical size and strength, the highest quality individuals would be expected to be bigger, at least for males (Kokko et al., [2002] note that physical size is partially influenced by testosterone). Physical formidability offers obvious advantages during bouts of intra-sexual competition, and it strongly predicts status in nonhumans; larger male baboons are ranked higher than smaller male baboons (Johnson, 1987), and larger individuals are more likely to win dyadic challenges in spiders (Taylor, Hasson, & Clark, 2001) and crayfish (Pavey & Fielder, 1996).

In human (males) there are two potential ways that physical size translates into higher status. The first is through a series of physical dominance displays between intra-sexual competitors. Larger males would, on average, win against smaller individuals, and larger individuals would rise to the top of hierarchies. Naturally, this need not involve actual physical combat. An individual's stature can be used as *information* regarding that individual's likelihood of success in competition, and confrontations are settled based on this information rather than actual combat, which would decrease costs for all parties involved. In this sense, stature can be thought of as a cue to intra-sexual competitive ability, and hence a critical piece of information in deciding who should be challenged and who should be deferred to. Recent developmental studies show that even before the end of their first year, human infants expect a physically larger individual to prevail over a physically smaller individual in a dominance contest (Thomsen, Frankenhuis, Ingold-Smith, & Carey, 2011). Hence, individuals of stature can simply avoid a status competition because they are not being challenged (see Figure 1).

This second is through physical size serving as a marker of someone's prestige.

Anthropological research suggests that physically stronger individuals may be better at procuring resources for the group, defend the group against hostile outgroups, and settle intragroup disputes (Von Rueden, 2014). Furthermore, there is evidence linking stature to health, intelligence, and political influence, which are prestige indicators (Blaker & Van Vugt, 2014). Height is positively associated with several variables associated with status, including income (Judge & Cable, 2004), military rank (Mazur, Mazur, & Keating, 1984) and authority in the workplace (Gawley, Perks, & Curtis, 2009). Furthermore, within businesses, individuals in managerial positions are on average taller than individuals in non-managerial positions (Egolf & Corder, 1991; Murray & Schmitz, 2011). Prestigious American science professors tend to be taller than the general public, and even the U.S. presidential elections are won by the taller candidate at a rate greater than chance (McCann, 2001; Stulp, Buunk, Verhulst, & Pollet, 2013). There is also evidence that being tall facilitates an individual's upward social mobility. A study involving pairs of brothers and sisters found that the taller sibling was on average better educated (Bielicki & Waliszko 1992). Different languages seem to reflect the relationship between stature and status; in various cultures, traditional and modern, leaders and other high status individuals are often referred to as "Big Men" (Van Vugt & Ahuja, 2011).

That people use height as a cue to others' placement in status hierarchies is demonstrated in a recent experiment showing that taller male and female managers are perceived as better leaders (Blaker et al., 2013). Whereas taller males were perceived as both more dominant, more intelligent, and healthier, taller females were only seen as more intelligent. This suggests that stature might lead to status benefits in both sexes, but that it does so via physical formidability more in men than in women.

There are other traits that might allow an individual to leverage physical formidability into status. A handful of studies have reported that fat free muscle mass -- which is estimated by running small electrical current through the body, and can be used as a proxy for physical strength -- is positively correlated with wages for both males and females (Böckerman, Johansson, Kiiskinen, &

Heliövaara, 2010; Bozoyan & Wolbring, 2011). Men's physical strength also predicts their quickness to anger and their likelihood of applying aggressive tactics to achieve their goals (Sell et al., 2009) -- thus being quicker to adopt a Dare strategy. Physical size at age three predicts aggressiveness and disagreeableness at age 11, which suggests that strategies relating to physical strength are calibrated early in life (Ishikawa, Raine, Lencz, Bihrlé, & Lacasse, 2001). Physically stronger men also endorse social norms that are beneficial to strong individuals. For example, Price et al. (2011) demonstrated that physically stronger men have a stronger preference for social hierarchies and status inequalities. Petersen et al. (2013) similarly found that upper body strength predicted men's endorsement of resource redistribution policies that favored them: Poorer men's upper body strength predicted stronger endorsement of wealth redistribution, whereas wealthier men's upper body strength predicted weaker endorsement of wealth redistribution.

Other traits that might relate to success in intra-sexual competition also convey high status. Facial masculinity -- which includes chin prominence, heaviness of brow ridges, and facial muscularity -- predicts career development of military officers, with these traits being associated with higher rankings within a military academy and more and quicker career promotions (Mueller & Mazur, 1996). The relationship between facial masculinity and success in hierarchical organizations might result from both the tactics that more facially masculine individuals employ (dominance) and the potential preferences for more facially dominant individuals as leaders (prestige). The latter is supported by evidence that individuals vote for a more facially dominant leader, especially in the context of war (Spisak et al., 2012).

Finally, physical attractiveness predicts a number of positive social outcomes afforded to higher status individuals, such as having more dates and friends and making more money (Roszell, Kennedy, & Grabb, 1989). In a study of college fraternities and sororities, more physically attractive individuals were perceived as more prominent and occupied high status roles in these student organizations more often (Anderson, John, Keltner, & Kring, 2001; Kalick, 1988). However, physical attractiveness was more strongly predictive of social status in men than in women, suggesting that

attractive women may have an edge in competition for mates but not necessarily in challenges for positions of leadership.

Verbal and Non-verbal Indicators of Status

In addition to leveraging physical capital into higher status, humans also employ various behavioral tactics to convey their status (although whether they do this deliberately remains to be seen). Consider a handshake. Shaking hands is a ubiquitous manner of introduction in the Western world, especially between men who meet for the first time. Something as simple as grip strength during a handshake might be an efficient manner of learning about another man's status. Socially dominant and extraverted individuals have firmer handshakes (Stewart, Dustin, Barrick, & Darnold, 2008). High status individuals are also more likely to have an open, relaxed posture, show less emotional expressivity in their face, and are less likely to laugh, especially in interacting with low status individuals (Ketelaar et al., 2012). In a lab study, participants who viewed individuals engage in subtly rude and norm violating behaviors rated these individuals as more decisive, strong, powerful, and in control (Van Kleef et al., 2011). In a review of the literature on nonverbal behavioral interactions, Argyle (1994) concludes that dominant individuals stand at full height with an expanded chest, hold a firmer gaze, speak in a low-pitched voice, and gesture more.

A lower voice pitch can also provide information about an individual's status as it is related to physical size and higher testosterone. Lower voice pitches are linked to status and occupational success (Puts, Hodges, Cárdenas, & Gaulin, 2007). Indeed, in a recent study on CEO's of companies registered on the American Stock Exchange showed that CEO's with lower the voices make more money, with a 25% decrease in voice pitch being associated with a \$187,000 increase in annual salary (Mayew et al, 2013). Men also lower their voice pitch when they are addressing another man who is lower in status, suggesting that voice pitch might be used to assert dominance in lieu of physical competition (Puts, Gaulin, & Verdolini, 2006). Finally, verbal expressions may differ between high- and low-status individuals. People are seen as more prominent and prestigious when they speak more clearly, louder, confidently, and directly, whereas those who speak more softly and pepper

their comments with nervous giggles are seen as lower in status (Fiske, 2010). Moreover, high status individuals often initiate conversations, shift discussions to their own areas of competence, and are more likely to interrupt other speakers in the conversation (Godfrey, Jones, & Lord, 1986; Mast, 2002). Finally, displays of emotions convey status differences. Group members who express anger are perceived to be of higher status than those who appear sad (Tiedens, 2001).

Status Changes and Emotions

Humans have likely evolved a suite of different emotional systems to negotiate positional changes in status hierarchies (Tooby & Cosmides, 2008). When individuals emerge victorious in a status competition (lower left cell of Figure 1) they experience happiness, elation and pride (Cheng, Tracy, & Henrich, 2010; Tracy & Robins, 2007). In contrast, a status loss (upper right cell of Figure 1) produces an increase in feelings of social anxiety, shame, rage, and depression (Gilbert, 1990). Moreover, identical behaviors can elicit starkly different affective sensations depending on the status consequences of the behavior.

Consider public speaking. As many readers of this chapter have experienced themselves, giving a research presentation to a group of undergraduate students results in less anxiety than giving the same talk to a mix of peers and more prestigious individuals at an international conference. Presumably, this difference in anxiety reflects the different status consequences of a good versus poor performance to the two groups, with poor performances in front of undergraduates not affecting status as much as a poor performance in front of a group of scholarly peers. Anxiety, or even the prospect of feeling anxious, might reflect the type of functional forecasting and simulation discussed by Tooby and Cosmides (2008). That is, simulating the aversive effects of actual status losses (i.e., experiencing anxiety) might lead individuals to either avoid situations in which they are likely to lose status or invest extra effort into winning such competitions. Similarly, people feel shame if they experience a loss in reputation, for example, after a moral transgression (Giner-Sorolla & Espinosa, 2011; Haidt, 2003; Tracy & Robins, 2006). On the other hand, when people lose a status competition that they feel they should have won, they may feel

rage, which might motivate them to seek a rematch or revenge. Finally, after experiencing a prolonged loss of status (e.g., unemployment), people may feel depressed, which motivates them to temporarily avoid any status competition until they have gained enough resources to status competitions. Depression symptoms indeed stop after people find a new job or start a new relationship, at which point they might have the capital to reenter the fray of status competition (Gilbert, 1990).

Other emotions could similarly guide behavior after status contests depending on the outcome of the competition, their status, and the status of their competitor (Figure 1). After winning a status contest, a high status individual might either experience pity or contempt for the low status person, depending presumably on how the loser responds to his or her defeat, or the manner in which the loser challenged the winner before the competition. In contrast, depending upon the reactions of the winner, low status individuals might display admiration when they feel they have legitimately lost the battle, and they might feel envy to motivate greater efforts during the next bout of competition.

Sex Differences in Status Striving

Like all mammals, men and women differ in their reproductive potential. Women invest more heavily in offspring (e.g., via the time and energy invested in gestation and lactation) and the number of years that they can conceive is constrained relative to men. Comparatively, men have lower minimal obligate investment in offspring, they can sire more offspring (with another partner) after a single act of conception, and they are reproductively viable for a longer period of their lives (Trivers, 1972). As a result, the ceiling of reproductive output is higher for men, and men's reproductive output tends to be more variable than female reproductive output (Bateman, 1948; Brown, Laland, & Borgerhoff Mulder, 2009). These differences in minimal obligate investment form the theoretical foundation for sex differences in mating strategies (e.g., Sexual Strategies Theory; Buss & Schmitt, 1993) and myriad related sex differences ranging from aggression (Archer, 1996; Daly & Wilson, 1988) to experiences of disgust toward unwanted sexual advances (Tybur, Lieberman,

Kurzban, & DeScioli, 2013). These sex differences also imply that there might be evolved sex differences in psychological status systems.

Male reproductive output is more variable than female reproductive output, but which males produce more offspring? As we discussed earlier, higher status males sire more offspring across several species (Ellis, 1995). An extreme example comes from the northern elephant seals living off the West coast of the United States and Mexico. Males compete for dominance before the breeding season starts, and the winners get exclusive access to females, whereas the losers are excluded from mating during the breeding season (Blaker & Van Vugt, 2014). Employing the game-theoretical model presented earlier (Figure 1), this means that the relative pay-offs for Dare versus Yield will be greater for male same sex interactions than for female same-sex interactions. The implication is that there is a stronger incentive for males to compete for status than for females because of the larger reproductive gains involved.

The relationship between male status and reproductive success also appears in humans. It was particularly strong in early complex societies, such as the Aztec, Inca, and Mesopotamian civilizations (Betzig, 1993). In these societies, access to women was strictly regulated, with higher status men enjoying greater access to women than lower status men. In the more egalitarian hunter-gatherer societies, the reproductive skew was arguably less pronounced, but the best hunters and political leaders nevertheless enjoyed more sexual affairs. Indeed, among contemporary Tsimane – a foraging people in the Bolivian lowlands in which pair bonding is normative – higher status men (both dominant and prestigious men) have more extramarital sexual affairs than lower status men (Von Rueden, Gurven, & Kaplan, 2011). The same applies to modern industrialized societies. Perusse (1993) investigated the relationship between the position of male employees and their sexual opportunities. The self-report data showed that employees with more senior positions had more sexual liaisons. Young male members of street gangs are reported to have more sexual affairs and greater status among their peers than non-gang members of the similar age (Palmer & Tilly, 1995). American World War II soldiers who returned home as war heroes - recipients of the Congressional

Medal of Honor – had more children than other veterans who did not receive this award (Rusch, Leunissen, & Van Vugt, 2014). This tendency for males to convert their high status into reproductive success is common enough to be labeled with a specific term: the Bathsheba syndrome (Ludwig & Longenecker, 1993).

Status, Mating, and Men's Psychology

Given the stakes of the outcomes of status competitions, men are expected to use more costly tactics to advance their own status goals. These tactics often involve dominance displays (e.g., physical fights; Archer, 2009), and they are often used in response to otherwise trivial threats – threats that only concern status rather than safety or tangible resources (Wilson & Daly, 1985). Further, aggressive responses to status threats appear to be used more by men when other men – other intrasexual competitors – are present to witness the outcome of the competition (Griskevicius, Tybur et al., 2009). Additionally, men gain status by participating in coalitional fights against other men of rival groups. Men contribute more to their groups in settings of intergroup competition than in the absence of intergroup competition, whereas women do not (Van Vugt et al., 2007). Men also report more aggressive intergroup encounters than women, and they are more likely to support and participate in between group violence (the male warrior effect; Van Vugt et al., 2007). Finally, men score higher on Social Dominance Orientation, which measures the extent to which people prefer status differences and unequal resource access between groups in society (Pratto, Sidanius et al., 1994). The direction of this sex difference is invariant across cultures, even appearing in relatively egalitarian societies such as Sweden and the Netherlands. Intergroup aggression may be a preferred tactic for especially low status males to elevate their status via combat, and therefore increase their access to resources (Chagnon, 1990; McDonald, Navarrete & Van Vugt, 2012; Navarrete et al., 2010).

Men may also apply prestige tactics to attract sexual mates. When groups of male participants were playing a public good game in a laboratory study and were being watched by an attractive woman, they donated more to the group fund than when there was no audience or when man audience (Van Vugt & Iredale, 2010). Additionally, men donate more to street beggars when in

the presence of female company rather than male company or alone (Iredale et al., 2008). Finally when men and women were primed with romantic motives and were then asked about their helping decisions, men endorsed engaging in heroic, status-enhancing forms of helping (e.g., jumping into water to help someone who is drowning; Griskevicius, Tybur et al., 2007). In contrast, women endorsed more conventional, low risk helping (e.g., volunteer work) after a romantic prime. In a virtual environment, men cross a scary rope bridge faster when observed by female bystanders compared to male bystanders (Frankenhuis, Dotsch, Karremans, & Wigboldus, 2010). Finally, men who are more committed to their current partner self-reportedly take fewer risks than men who are less committed to their partner (Frankenhuis & Karremans, 2012).

Status and Women's Psychology

If men's status conveys information regarding benefits to women (e.g., as mates), then selection might favor a female mating psychology that finds status attractive. In Buss's (1989) landmark cross-cultural study on mate preferences, females across cultures valued status relevant traits in a romantic partner (e.g., earning capacity, ambition) more than men. In lab studies, females express greater sexual interest in dominant men, but men do not express greater sexual interest in dominant women (Sadalla, Kenrick, & Vershure, 1987). When asked to "build a mate" using a limited budget, women prioritize status and resources in constructing their mate more than men (Li et al., 2002). Men are not blind to this preference; they are more likely to advertise their status and resources on personal romantic advertisements relative to women (Pawlowski & Dunbar, 1999).

Women's mate preferences for status could reflect both preferences for the direct (i.e., protection and resources) and indirect (i.e., heritable quality) benefits that high status men might possess. The former is certainly true, with women prioritizing social status and resources more in long-term mates relative to short-term sexual partners (Li & Kenrick, 2006). The latter also appears to be true. For example, women's preferences for the type of dominant facial structures described previously are highest at peak fecundability (Johnston et al., 2001; Penton-Voak & Perrett, 2000), as

are preferences for men's intrasexually competitive behaviors (Gangestad et al., 2004). Further, preferences for such traits are often observed only when female participants judge attractiveness as a short-term sexual partner (see Thornhill and Gangestad, 2008, for a theoretical overview; see Gildersleeve et al., 2014, for a recent meta-analysis). The data suggest a clear picture – women prefer status, resources, and morphological and social dominance displays in men, both for the direct and indirect benefits that these traits afford.

A final note on sex differences is that men and women might follow different tactics to acquire status. In one study, men and women rated the social desirability of many different dominance acts (Buss, 1981). The main conclusion is that men are more accepting of egoistic dominant acts such as “Managing to get one's way” or “Complaining about having to do a favor for someone.” Women were more accepting of more prosocial, prestigious acts such as “Being active in many community and campus activities” or “taking charge of things at the committee meeting.”

The Evolutionary Psychology of Leadership

The final section focuses on one particular hierarchical position in groups: leadership. Leaders enjoy considerable prestige in most human societies, and the associated benefits should make leadership positions particularly attractive (Van Vugt, 2006). The dynamics of leadership are complicated, though, and not all individuals seek out leadership positions, and not all leaders are afforded similar status. Evolutionary biologists have had an enduring interest in leadership, and there is a growing literature on the subject dedicated to unravelling some of these complications (e.g., King et al., 2009). Although leadership has been and continues to be a hugely popular theme in the social sciences, this literature has traditionally not addressed fundamental questions about leadership, such as why individuals allow leaders to emerge, why individuals would incur the costs of taking up leadership roles, etc. Following Price and van Vugt (2014), we view the topic as a reciprocal exchange between leaders and followers where status and prestige benefits accrue to individual leaders as they provide public goods to followers.

Service-for-Prestige

In human societies, leaders are often highly respected, liked, and admired, with Nelson Mandela and Mohandas Gandhi serving as peak examples. This stands in stark contrast with the highest status individual in non-human primate groups such as gorillas and chimpanzees where dominant males (alphas) appear to be feared and, at the risk of anthropomorphizing internal states, loathed by lower ranking individuals (King et al., 2009; Van Vugt, 2006). Also leaders in human groups cannot monopolize resources to the same degree as the alpha in non-human primates. This raises a critical question: if human leaders do not dominate access to resources as non-human primate alphas do, but they still invest disproportionate resources into their groups, then why would they seek out and accept such positions? The service-for-prestige theory (Price & Van Vugt, 2014) contributes to solving this puzzle.

Human leadership is characterized by voluntary, reciprocal arrangements between leaders and followers (cf. Trivers, 1971). In this reciprocal dynamic, leaders trade their expertise, skills, education, personal risks, and time in exchange for prestige offered by followers. This dynamic works best for followers when power differentials between leaders and followers are small, thus when leaders have limited opportunities to use their position to exploit followers. Situations in which power differentials between leaders and followers are large tend to produce status hierarchies based on dominance rather than prestige (Van Vugt et al., 2008). Furthermore, giving prestige benefits to leaders poses a collective action problem among followers as it is cheaper to profit from leaders' group contributions while not deferring to them. To the extent that groups are better at solving this free-rider problem this will facilitate good leadership.

Several observations support the service-for-prestige idea. First, individuals who achieve leadership positions in foraging societies often do so via public displays of expertise (e.g., hunting, political influence). Among Amazonian Shuar, individuals who are perceived as providing the most valuable service to their social groups are preferred as group leaders and receive more esteem from

others in the group (Price, 2003). Lab experiments similarly show that participants who demonstrate a willingness -- and ability -- to provide benefits to the group receive more status (Anderson & Kilduff, 2009; Hardy & Van Vugt, 2006; Willer, 2009). Finally, the status benefits associated with taking on leadership roles are often converted into reproductive success (Von Rueden, 2014).

Second, traits valued in leaders in Western societies include intelligence, vision, persistence, communication skills, persuasion, fairness and ethical decision making (Judge, Colbert, & Ilies, 2004). These are also among the leader traits most valued by followers within traditional societies (Tooby, Cosmides, & Price, 2006; Von Rueden, 2014). This suggests that there is cross-cultural consistency in what followers expect from leaders (Den Hartog et al., 1999). Communication and oratory skills facilitate social coordination, higher intelligence would conceivably relate to better decision-making, and fairness would guard against exploitation of followers (Van Vugt et al., 2008).

A third observation in line with service for prestige is based upon considerations of the costs that leaders can impose upon followers (Padilla, Hogan, & Kaiser, 2007). As leaders accumulate power over time, their positions in status hierarchies can transition from prestige based to dominance based as they can start to monopolize resources. In mutually beneficial reciprocal relationships between partners of relatively equal power, individuals are partially motivated to treat their partners well, because poor treatment can lead the partner to exit the relationship and devote resources elsewhere (Van Vugt et al., 2004). As individuals become more dependent on leaders for organizing collective action and the distribution of resources, they become less able to leave the relationship, hence leaders' incentives to treat their followers fairly decreases. With increases in group size and population density, and, perhaps most importantly, decreases in population mobility, leaders can accumulate power more easily, and leader-follower relationships can transition toward being dominant and exploitative. This is especially the case when levelling mechanisms that might rein in power abuses such as criticism, salary caps, and replacement of leaders are absent (Boehm, 1999; Van Vugt & Ahuja, 2011). The consequences of such shifts in power are underscored by the

psychological literature, which suggests that increases in power decreases empathy (Galinsky et al., 2006) and increases abuse (Kipnis, 1972). Furthermore, anecdotal reports suggest that among the higher echelon leaders in politics and business, there is a preponderance of males with dark triad personalities – a combination of Machiavellianism, narcissism, and psychopathy (Babiak & Hare, 2006; Ludwig, 2002).

Conclusions

By analyzing status from an evolutionary perspective, this chapter attempts to make various contributions to the literature. First, it distinguishes status from a number of related constructs that are often used interchangeably in the literature, including power, dominance, prestige, and leadership. Second, it differentiates conceptually status hierarchies from decision-making hierarchies. Third, it contributes to a foundation for better understanding status via an adaptationist lens by considering the origins, functions, development, and psychological mechanisms underlying status striving in humans, partially by viewing status competitions via a simple game theory model. In doing so, it highlights distinctions between evolved psychological systems for signaling status, assessing status, managing status change, and converting status into reproductive opportunities. Fourth, it highlights the role that hormones, physical attributes, and emotions can play in facilitating individuals' positions in status hierarchies.

Although we have endeavored to cover a wide range of topics on status, this chapter has also been limited in scope, partially based on outstanding questions that have yet to be solved. Notably, we have not examined the causes of the variability in status hierarchies between human societies, and between humans and nonhumans. Yet it is clear that some societies (and species) are more hierarchical than others. Theorists have asserted that hierarchies are attenuated when (a) resources are more difficult to monopolize, (b) sharing resources is essential for survival, (c) individuals can easily leave groups, and (d) form coalitions to overthrow a dominant. Further work should investigate the importance of these levelling mechanisms in the formation of status hierarchies

(Cashdan, 1983; Plavcan, van Schaik & Kappeler, 1995). Additionally, more work can be done on the game. Our treatment of the Chicken game implied two different phenotypes. Yet there is naturally great variability in human personality (Buss, 2009; Nettle, 2006), which might partially reflect frequency-dependent selection on dispositions analogous to the two status strategies. Future research could test the degree to which heritable personality variation relates to behavior in status competitions (cf. Verweij et al., 2012). Third, our treatment of female status striving has been limited (see Campbell, this volume, for an in-depth treatment of female status). The literature describing female intrasexual competition is building (e.g., Beneson, 2013; Campbell, 1999, 2013; Grant & France, 2001; Hess & Hagen, 2006; Pusey, 1997), but more work is required to elucidate the effects of intra-sexual competition on losers and winners in female-female contests, and, ultimately, the fitness benefits that women procure by moving up female-specific status hierarchies. Other lines of research might further investigate status striving tendencies throughout the lifespan of humans, and the different tactics to gain status by older and younger individuals (Wilson & Daly, 1985). Answering questions such as these can shed light onto the psychology of human status, and can help us understand questions regarding the evolutionary foundations of status hierarchy.

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Figure 1. Chicken: A Game of Status

		Player 2	
		Yield	Dare
Player 1	Yield	2, 2	1, 5*
	Dare	5, 1*	-1,-1

Note. Payoffs are for Player 1 and 2, respectively; Yield and Dare constitute alternative game strategies (underpinned by genes); game equilibria are indicated with asterisks.