

**Translating Socioeconomic Status between Non-Human Primates and Human Studies in  
Health Research**

Rosalind B. King<sup>1</sup> and Annika Paukner<sup>1,2</sup>

<sup>1</sup>*Eunice Kennedy Shriver* National Institute of Child Health and Human Development, National  
Institutes of Health

<sup>2</sup>Department of Psychology, Nottingham Trent University

**Author Note**

Rosalind B. King <https://orcid.org/0000-0002-4832-8641>

Annika Paukner <http://orcid.org/0000-0002-3421-1864>

We have no known conflict of interest to disclose.

Correspondence concerning this article should be addressed to Rosalind B. King,  
Population Dynamics Branch, NICHD, 6710B Rockledge Drive, Room 2305, Bethesda, MD 20892-  
7002. Email: rozking@mail.nih.gov

We discuss theoretical considerations for the development of appropriate animal models of socioeconomic status (SES) to study its effect on health and development, with an emphasis on the literature on non-human primates. Existing evidence supports the proposition that early childhood adversity has long-term health implications. Experimental research on the effectiveness of social policy interventions provides the gold standard of evidence but is difficult to obtain using humans. Animal models may play a role in generating a mechanistic evidence base, but researchers need appropriate models of SES. Focusing specifically on the potential for translation between animal and human models, we define SES conceptually and outline its links to health. We then note demonstrated areas of equivalence and potential limits. We conclude with promising open questions for which answers would hold great utility.

Social interventions to address the long-term developmental impacts of socioeconomic status have received a great deal of popular and scientific attention (Campbell et al., 2014; Furman, 2015). Research in humans has established a correlational link between negative experiences associated with low socioeconomic status in childhood, particularly early life adversity (often operationalized as maltreatment, neglect, parental absence, or economic deprivation), and adult health outcomes such as cardiovascular disease risk and mental illness (Marmot, 2005; Rahkonen, Lahelma, & Huuhka, 1997; von Rueden et al., 2006). Policy makers seek an evidence base before implementing expensive policy changes such as income support programs, but it is difficult to model the biological mechanisms underlying these associations due to the complexity of human social and behavioral patterns, the length of the human life span, and ethical considerations (e.g., no random assignment to exposure to early life adversity). Studying existing human populations at a single point in time produces valuable sets of correlational data, but the causal relationships remain unknown. “Natural experiments” in which a randomly selected group of individuals receives an income boost due to an outside event are a feasible alternative but occur only rarely (Costello, Compton, Keeler, & Angold, 2003; Jones-Smith, Dow, & Chichlowska, 2014). Random assignment to interventions to reduce early life adversity are possible, but running such a trial with sufficient statistical power is exactly the type of expensive effort that requires preliminary studies to support effectiveness before making the investment.

Animal models of social behavior can be useful when they are able to approximate the complexity of human systems. Animal models have great utility in that they make inference less complex, but such simplicity can come at the price of a lack of translatability. Most importantly, the use of animals in research is also subject to ethical constraints, but with different

considerations (National Research Council, 2011). Research animals must receive adequate nourishment, shelter, and medical care. But we do not assign to them rights to select their mates, choose their dwellings, or prepare their own food. We are able to track their every action and manipulate their ability to go at will between confined spaces and the environment around those spaces. They must have mental stimulation, but they have no expectation of pursuing formal education or employment. Animals can be used in randomized controlled trials of status or mating opportunities and their environments can be manipulated to isolate single mechanisms of interest. Most animals also naturally have faster life cycles than humans, so experimental longitudinal, developmental, and intergenerational research is feasible within a shorter study period.

Animal models in this respect offer opportunities for functional validation of theories or mechanisms of social interventions that cannot be experimentally manipulated in humans. Isolating the mechanisms underlying a social intervention and pre-testing the causal processes in an animal model may provide a cost-effective way of directing investment into the interventions most likely to succeed. Here we outline considerations of how animal models of social stratification, primarily with non-human primates (NHPs), might translate to human systems of socioeconomic status and thus provide a context for testing these mechanisms. We acknowledge that multiple animal models could advance this goal; indeed, there is a vast literature on rodent models that provides valuable and important insights into underlying biological mechanisms. However, we focus our discussion on NHPs whose patterns of complex social behavior, including an extended juvenile period and co-residence with families of origin even after sexual maturity, are more similar to human life course development (Phillips et al, 2014).

### **The Meaning of Socioeconomic Status in Humans**

The term socioeconomic status (SES) refers to an individual's standing relative to others in a community in terms of their access to power with which they can obtain resources (McLoyd, 1998). Rewards and privileges related to economic means and social prestige are typical elements of the construct (Mueller & Parcel, 1981). In practical terms, indicators of SES include access to financial capital (material resources such as household income), human capital (nonmaterial resources such as education), and social capital (nonmaterial resources derived from connections to family, friends, and other social affiliates) (Bradley & Corwyn, 2002). Observable characteristics that proxy for or demonstrate SES are traditionally divided between those that are ascribed ("assigned at birth" – citizenship, caste) versus achieved ("earned over the life course" – education, income, occupational prestige). Markers of SES are variable across generations and within an individual's life course. For example, children have not yet completed their education and are therefore usually assigned their parents' characteristics until they reach their own adulthood. Current SES may thus not accurately reflect an individual's cumulative experience, especially in cases of intergenerational mobility.

Humans with high SES can be more effective than those with low SES of achieving objectives through their greater ability to obtain and use resources. Both relative and absolute position on the SES ladder have implications, as well as relative positioning within SES groupings (Marmot, 2005). Absolute status may matter more in a situation of great deprivation when basic needs are not met and high SES may help to overcome physical limitations. Status relative to peers may exert a greater effect above a minimal level of subsistence. Relative status has been mostly studied in adults, but emerging research indicates that children have an awareness of their position relative to their peers and adolescence may be a particularly sensitive

time for measuring oneself against others (Odgers, 2015). Both dimensions of SES may therefore significantly affect health outcomes across developmental stages.

### **Aspects of SES That are Most Relevant for Health Research**

Researchers have documented a positive correlation between experiences linked with SES and health. While significant adverse childhood experiences (e.g., abuse and trauma) are justifiably of great concern to researchers, policy makers, and community members alike, scientific evidence suggests that more typical negative experiences associated with living with socioeconomic disadvantage also have deleterious effects. For example, lack of access to prenatal care correlates with asthma and obesity at age 5 years (Noonan, Corman, Schwartz-Soicher, & Reichman, 2012). Parental income and education from low to high values correlate with features of children's brain structure (Noble et al., 2015). But it is unclear how the effects of SES on health play out across different phases of the life cycle. Childhood experiences could shape adult health through a range of exposures and potentially relevant time periods (Cohen, Janicki-Deverts, Chen, & Matthews, 2010) and the effects might be mitigated by well-timed interventions (Brody et al., 2017). Variable physical conditions in housing (e.g., crowding), neighborhoods (e.g., noise), and schools (e.g., ventilation) as well as psychosocial exposures, including parents' mental health status, violence, and chaos, are all theorized to impact health outcomes. The relative importance of timing and duration of exposures can be understood through conceptual models of specific developmental periods, accumulation over time, and direction of change across stages of childhood.

Scientists are confident that the social gradient in health exists, but less sure about the causal chain. A recent study (Foverskov & Holm, 2016) used nine waves of data collected from British adults ages 30-60 years with annual assessments of health and SES to try to tease apart

three models of causality: social causation (SES generates health outcomes through factors such as stress and lack of resources), health selection (health history leads to current SES), and indirect selection (factors prior to both current SES and health outcomes are the underlying cause of the observed correlation). The results support the indirect selection hypothesis and imply that early life experiences generate both SES and health in adulthood.

Theories of the long-term impact of childhood experiences associated with SES on adult health extend to possible intergenerational effects. The theory of the developmental origins of health and disease, grounded in the Barker hypothesis of fetal adaptation to deprived environments (Barker, 1997), posits that facets of maternal health such as stress and nutritional status impact fetal development and subsequent health across the life course. Adversities such as chronic stress and limited resources are encountered more frequently by women living in low SES circumstances than those in high SES environments (Kim & Wickrama, 2017). Thus, maternal SES literally imprints itself in the child's physiology, potentially including epigenetic effects (De Boo & Harding, 2006).

### **Equivalents to SES in Model Animal Research**

Theoretical perspectives can help us understand better how animal models of SES may be appropriate and useful. Socioeconomic status is a characteristic which an individual carries into a structural system of social stratification. The nature of that system shapes how individuals with varying levels of SES interact and are able to change their SES. For example, the conflict theory of social stratification sees a hierarchy in which the powerful few exploit the many, usually by controlling capital such as the best places to sleep or the attention of the alpha male. The functionalist perspective purports that societies need members to fill different roles, and members of society should occupy the positions for which their talents make them best suited. In

this view, social stratification is not a struggle between members who are competing for the same goal, but rather a collaborative agreement in order for society to function.<sup>1</sup> In the former, high ranking individuals must routinely engage in actions to suppress subordinates; in the latter, competitive stress is less present and low ranking individuals settle into their position of subordination. Such theories lead to the selection of an appropriate species for study. For example, testing the conflict approach may require NHPs such as rhesus macaques who enforce the social status superiority of high-ranking individuals via aggression directed at low-ranking individuals (Sapolsky, 2005). Testing elements of the functionalist approach may require species such as hamadryas baboons who live in multilevel social structures (Swedell & Plummer, 2019) or marmosets and tamarins who are known for the division of labor between and within the sexes (Snowdon & Ziegler, 2007).

Animal models may be evaluated according to different types of validity beyond the essential starting point of face validity. Construct validity, a measure of the underlying meaning of the model, requires a form of external validation such as comparison to a known measure of the phenomenon under study (e.g., stress as measured by heart rate variability or patterns of cortisol expression in both human and non-human animals). Construct validity is higher if cross-species homology can be demonstrated, which is more likely for models of animal behavioral patterns that share a close phylogenetic relationship with humans (Phillips et al, 2014). Finally, predictive validity - how well future behaviors or outcomes are predicted - is the gold standard (e.g., symptoms consistent with schizophrenia in rats are ameliorated by drugs known to treat schizophrenia in humans [Millan & Bales, 2013]). When considering behavioral characteristics

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<sup>1</sup> These theories have been the subject of explication and empirical research for decades in sociology. For an example of a foundational citation, please see Parsons (1949).



of animal models, characteristics should be measurable and as close as possible to the human mechanisms of interest.

Another initial question is whether the model should be grounded in shared pathways (such as intra-group processes of competition or intergenerational transmission of status characteristics) or shared structures (such as group-level patterns of coordinated activity). It is necessary to consider the range of the repertoire of behaviors relevant to the constructs of choice, the neurological or other biological bases of those constructs, the possible measurements in both human and animal models, and the translational measures available to researchers. A complete model of SES in animals may not be possible, but individual components may provide crucial insights into the formation and outcomes of SES in human populations. For example, social status hierarchy – social organization involving ranking from high to low – appears to easily lend itself to a model of dominance and power (Chiao, 2010). Rodents and NHPs tend to live in social groups with a high degree of heterogeneity of dominance.

Species of NHP have social systems across the spectrum of variation from highly despotic to highly egalitarian. In the former, low status is often reinforced by aggressive behaviors (i.e., physical threats) from high-ranking group members, leading low-ranking animals to avoid highly desirable locations out of anticipation of attack. Some humans still use aggression in private to reinforce social hierarchy (particularly around gender), but public expressions of violence are generally stigmatized in Western societies and authority for public aggression is limited to government entities (Collins, Saltzman Chafetz, Lesser Blumberg, Coltrane, & Turner, 1993). Non-violent discriminatory actions such as microaggressions may be analogues for NHPs' agonistic expressions of dominance such as claiming public spaces and performative rituals reinforcing submission to authority (Collins, 2000).

Social status also relates to access to resources such as food, social partners, or resting places. Although arguably access to resources in captivity is not a good model for the human experience since minimum standards of animal welfare must be met, it remains an open question whether the responsible mechanisms can only be uncovered under conditions of extreme disparity or whether limited or reduced access can suffice. Typical animal diets in captivity are limited when compared to the diet choices of humans, and high- and low-ranking animals do not necessarily differ in the quality of food. But an animal model of differential food consumption in terms of access to and amount of food (above the minimum) may approximate high- and low-caloric portion sizes commonly associated with human SES. Wild populations, especially territorial animals, experience greater resource limitations than captive populations and might be good models for resource-related effects. Studies with wild NHPs indicate impacts on primates' health from low social status through shorter lifespans, delayed reproduction, lower glucocorticoid levels, and less protection from drought effects (Bercovitch & Strum, 1993; Sapolsky, 2005; Zippel, Archie, Tung, Altmann, & Alberts, 2019), which are likely the results of both psychosocial and resource-mediated effects.

Control over captive settings also lends itself to testing hypotheses of controllability and predictability of the environment. For humans, individuals with high SES perceive themselves to have high efficacy and autonomy with regard to their surroundings compared to individuals with low SES (Boardman & Robert, 2000). While we cannot clearly measure animals' perceptions of these qualities, it is certainly possible to manipulate animals' control over the course of their daily routine. For example, the limited bedding paradigm can intermittently restrict a rodent's ability to care for her pups, which results in erratic maternal behavior that evokes an experience of chaos for the offspring (Walker et al., 2017). Another model of access to resources which are

actively selected by the offspring themselves could be the availability of enrichment items like preferred toys which can be varied by developmental stage.

Some behavioral researchers working with animal models have focused on the impact of status ranking on health. Rodents and captive NHPs may provide models for the physiological changes related to instability in social hierarchies because their dominance rankings can be manipulated. For example, among rhesus monkeys, instability in the composition of daily social groups is associated with decreased performance of the immune system (Capitanio & Cole, 2015). Other studies have shown that epigenetic changes are related to NHPs' ranks (Tung et al., 2012), mother's rank can significantly affect neurobehavioral outcomes (Suarez-Jimenez et al., 2013), and biological outcomes track current social status. Researchers can also vary NHPs' and rodents' social partners and mating opportunities according to the variable of interest (personality, care-taking behavior, dominance status) and even maternal rank via cross-fostering paradigms. In this way, animals present opportunities to conduct prospective randomized control trials of status (trajectories and point-in-time) and mating (McCormick et al., 2017).

Animal models can also be particularly useful for capturing the biological effects and mechanisms of SES, which are difficult to measure in humans when they rely on invasive measurements (e.g., venipuncture, biopsy). Animal models are further enhanced by animals' faster life cycles – particularly mice and rats – which can reduce the costs and investment of intergenerational studies. However, studies that require very large sample sizes (e.g., genomic and epigenomic mapping studies) may continue to be more cost effective to conduct in human populations.

### **Limits of Animal Models that Seem Unsolvable**

Some aspects of the human experience seem too complex to translate across species. For example, human reproduction occurs within a context of socially structured partnering patterns, sexual activity behaviors not tied to ovulation, and the ability to use technology to prevent conception or terminate gestation. Recent work in rats appears to show an effect of adolescent status on adult male attractiveness but the findings did not apply to a “competitive mating context” (McCormick et al, 2017). Notable differences also exist in the pace of reproduction and the dependency period of offspring.

Another limitation of animal models is the greater complexity of emotion and motivation demonstrated by humans. Parental buffering of stress and fear in young offspring is a common phenomenon across species, but it is not clear whether the dampening shift in its effectiveness experienced by human adolescents occurs in rodents and monkeys (Gunnar, Hostinar, Sanchez, Tottenham, & Sullivan, 2015). Animals generally use physical methods such as agonism, including aggression, to express dominance. The blunt techniques of agonistic display and submission may be relevant to models of bullying in childhood. In contrast, the increasingly sophisticated breadth of the behavioral repertoire available to humans as they age allows dominance to be transmitted through more nuanced methods ranging from linguistic subtleties to emotional control to social media sharing.

Humans also demonstrate behaviors of self-sacrifice whose existence in animals, including chimpanzees and rats, is controversial (Marshall-Pescini, Dale, Quervel-Chaumette, & Range, 2016). Instances of parents fulfilling their children’s nutritional needs before their own are well-documented in humans but less common in animals. A recent attempt demonstrating pro-sociality around food in canines showed a dependence on familiarity with the beneficiary which does seem to follow human behavioral patterns (Marshall-Pescini, et al.).

Studies link loneliness in both humans and NHPs to poorer health (Hawkley & Capitano, 2015). Animal models of loneliness appear to have links to relative position in the social hierarchy, but it is not clear that loneliness in humans varies systematically by SES. High SES humans do appear to have unique positions within social networks (Luo, Morone, Sarraute, Travizano, & Makse, 2017) and hierarchical species of NHPs such as rhesus macaques may be able to replicate patterns of social status and network centrality across developmental stages (Wooddell, Kaburu, & Dettmer, 2019). These models in infancy and adolescence have the intriguing ability of modeling children's own status rather than remaining within the paradigm of assigning their parents' status to them. But the qualitative nature of social isolation may vary beyond intersecting characteristics such as gender and life course stage in humans in ways that are impossible to replicate in animals such as balancing work-family conflict at mid-life.

Other 'human-unique' aspects of SES may be the accumulation of wealth, educational attainment, or access to and engagement with social institutions. Furthermore, humans belong to multiple non-overlapping hierarchies (e.g. work, home, friendship network) with different roles and demands placed on the individual in each position. Humans may also share social status with others. In contrast, NHPs and rodents tend to have a singular social hierarchy and a clear understanding of their standing in relation to others. In rhesus macaques, for example, no two animals sharing the same rank within the same group. Potentially, researchers could model multiple systems of stratification in humans as multiple family lines in one animal community (e.g., Swedell & Plummer, 2019). However, their most complex social hierarchies may still not reach the same level of complexity and interactivity as human SES systems.

The direction of outcomes related to SES may also differ between humans and animal models in nuanced ways. For example, while low levels of maternal care or more extreme

stressors such as abuse are associated with younger age of menarche in girls and female rodents, the direction of the relationship between early life stress and pubertal onset in boys and male rats is still unclear (Cowan & Richardson, 2018). The relationship between low status and the onset of reproductive function appears to work in the opposite direction in NHPs (Wilson, 1992). Going beyond face validity may be crucial. If the mechanisms of these features can be identified in humans, it may be possible to further test the same mechanisms in animal models to ultimately translate back to humans. Moreover, the conceptual models must be theoretically grounded to place the mechanism within the larger process.

### **Conclusion**

Animal models can help illuminate how perceived stress and emotional responses to psychosocial environmental exposures are reflected in stress-sensitive biomarkers and pre-disease markers which in humans are associated with negative experiences that tend to correlate with lower SES. Small animal groups can be created as a model for a range of human stress-induced outcomes including socioemotional behavior, reward deficits, disordered eating, substance use, susceptibility to infection, disrupted neurobehavioral development, cardiovascular disease and stroke, and reproductive compromise. Animal models appear ideal for research on intergenerational and prenatal factors due to ease of manipulation and animals' faster life cycle. Challenges include balancing the attractiveness of a short length of generation against the speed of aging (Phillips et al., 2014) so that developmental mechanisms are not so accelerated as to prohibit translation to humans.

The focus of many animal studies on the effects of high or low status do not address the potential impact that middle-level status may have on stress and health (Sapolsky, 2005). Findings based on the prevalent model of early adversity in animal research, particularly the

focus on maternal licking or circumstances of maternal neglect in rodents, do not clearly translate to the broader range of human parent-child interactions and status-related experiences in childhood (Perry et al., 2019). Similarly, there are multiple rodent models for mental health disorders (Millan & Bales, 2013), but less considered is whether psychological well-being can also be modeled.

Ultimately, the links between SES and health in humans are well-documented, but we still lack an understanding of the responsible mechanisms. For example, behavioral economists are conducting experimental work on time preferences and delay discounting that may explain how individuals in poverty become trapped in a financial cycle of trading future benefits for short term rewards (Haushofer & Fehr, 2014). Models in rodents and NHPs are very good at capturing isolated processes, so while creating a complete animal model of human SES may not be feasible, ethically conducted research using these models may still provide useful mechanistic evidence and theoretical validation.

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