



Review article

Age-related social selectivity: An adaptive lens on a later life social phenotype

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ABSTRACT

Age-related social selectivity is a process in which older humans reduce their number of social partners to a subset of positive and emotionally fulfilling relationships. Although selectivity has been attributed to humans' unique perceptions of time horizons, recent evidence demonstrates that these social patterns and processes occur in other non-human primates, suggesting an evolutionarily wider phenomenon. Here, we develop the hypothesis that selective social behavior is an adaptive strategy that allows social animals to balance the costs and benefits of navigating social environments in the face of age-related functional declines. We first aim to distinguish social selectivity from the non-adaptive social consequences of aging. We then outline multiple mechanisms by which social selectivity in old age may enhance fitness and healthspan. Our goal is to lay out a research agenda to identify selective strategies and their potential benefits. Given the importance of social support for health across primates, understanding why aging individuals lose social connections and how they can remain resilient has vital applications to public health research.

Across post-industrialized societies, humans tend to reduce their number of social partners with age and focus on emotionally close and fulfilling partners (Wrzus et al., 2013). Prevailing theories to explain this social aging phenotype, i.e. age-related social selectivity, posit that individuals' perception of future time horizons motivates social choices such that less remaining time leads to selective investment in emotionally fulfilling relationships (Carstensen, 2021). Recent evidence, however, demonstrates that many non-human primates also exhibit age-related declines in sociality (Machanda and Rosati, 2020; Siracusa, Higham et al., 2022) and that some focus on more positive relationships in old age (Rosati et al., 2020; Siracusa et al., 2022). If these patterns of behavior are not unique to humans, it suggests a need to consider broader adaptive explanations for the emergence of age-related social selectivity prior to the evolution of humans' advanced cognition. In this review, we examine the hypothesis that social selectivity is an adaptive strategy to accommodate the changing costs and benefits of social interactions that accompany aging. We start by defining age-related selectivity and address the key challenges of evaluating whether the patterns of social aging observed in non-human primates (hereafter, "primates") are driven by selectivity per se or emerge as a byproduct of aging and demographic phenomena. We further identify emerging evidence of age-related social selectivity within primates. We

then outline potential adaptive benefits of social selectivity in old age and their behavioral and physiological mechanisms. We conclude by identifying critical predictions and areas for research into the potential adaptive benefits of age-related social selectivity and the implications of this work for understanding risks of social isolation in humans.

Social grouping and social behavior evolve in response to a range of environmental challenges and entail both benefits and costs. Individuals form positive, friendly relationships ("ties") that extend over time and whose qualities are often measured in terms of their frequency of interaction ("strength") or reported feelings of affection ("closeness"). Such ties also situate individuals within broader networks of indirect connections (Brent, 2015). Strong ties and integration within networks increase survival and reproductive success in a wide range of social animals (Ostner and Schülke, 2018; Thompson, 2019), including humans (Holt-Lunstad et al., 2010). In humans, close ties and integration are broadly conceptualized to improve health and fitness by offering direct and risk-buffering support in the forms of information, material aid, and emotional security, among others (Cohen and Wills, 1985; Page et al., 2017). Across primates, ties clearly offer cooperative support to access resources, maintain social status, protect from harassment and environmental exposures, and help in rearing offspring (Thompson, 2019). Nevertheless, social living inherently increases

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competition for resources (Alexander, 1974; Wrangham, 1980) and exposure to pathogens (Nunn, 2012; Page et al., 2017), and maintaining social ties may themselves pose costs, such as time and energy investments, risks of injury or defection, and conflicts over resource distribution (Kummer, 1978).

The costs and benefits of sociality vary over the life course, and individuals' physical and cognitive function are expected to pose increasing constraints during senescence. Although varying in kind and degree, age-related declines in these functions are ubiquitous across primates. Aging humans (Maresova et al., 2019) and their closest relatives bonobos and chimpanzees (Emery Thompson et al., 2020b; Lowenstein et al., 2016; Morbeck et al., 2002), experience declines in lean muscle and skeletal health and decrease their demanding physical activity. Primates experience immunosenescence, such that adaptive immune function decreases with age as innate inflammatory responses increase (rhesus macaques, Chiou et al., 2020; Cooper et al., 2022), and older individuals are more susceptible to infection (chimpanzees, Emery Thompson et al., 2018; Pera et al., 2015; Phillips et al., 2020; Scully et al., 2018). Executive cognitive function generally declines with age in primates, including deficiencies in storing and manipulating short term memory, shifting attention across tasks, and updating information during action (cross-primate review, Lacreuse et al., 2020). In vervet monkeys, age-related declines in executive function drive decreases in social effort and do so more strongly than impaired physical function (Negrey et al., 2023). In chimpanzees, such declines also encompass aspects of social cognition, such as gaze-following and using cues of a social partner's attentional state (Lacreuse et al., 2014). Aging primates also experience neuroanatomical changes, such as neuron loss and development of β -amyloid plaques, that correspond with cognitive deficits (gray mouse lemur, Chaudron et al., 2021; chimpanzees, Mulholland et al., 2021; rhesus macaque, Peters and Kemper, 2012; macaque spp. Youssef et al., 2016), physical impairments (vervet, Frye et al., 2021), and deficits in hearing and auditory processing (rhesus macaques, Gray and Barnes, 2019).

Such declines in function associated with aging hinder social interaction and permeate an individual's social world, both as a social partner and actor. Older individuals may experience different or reduced benefits from social relationships, leading to changes in social motivation. For example, many younger individuals use social relationships as a means to explore opportunities and learn about the world, while older individuals have already accumulated such knowledge (Wrzus et al., 2013). Aging individuals may also pursue alternative strategies to achieve their reproductive goals, such as the greater use or abandonment of aggressive coalitions (Setchell, 2008).

We expect high selection pressure for social strategies that avoid costs and optimize reproductive success and inclusive fitness in old age, given that many long-lived primates spend a considerable portion of their lives in a post-prime state. Although spending time alone is one way to mitigate social costs and manage constraints, general isolation is not a productive option for most social animals. Living in close and long-term association with conspecifics provides an array of advantages, including predator avoidance and access to resources (Silk, 2007). Further, social isolation causes a suite of biobehavioral responses that are deleterious when maintained over the long term, including heightened hypothalamic pituitary adrenal (HPA) axis activity and vigilance, and can feedback to reduce the ability to establish future social connections when needed (Hawkey and Cacioppo, 2010; Layden et al., 2018; C. R. Lee et al., 2021). It is therefore likely that social contact retains some value at all ages for individuals of social species. Instead of isolating in response to constraints and costs, individuals may associate with key social partners that support their reproductive goals and buffer them from negative experiences.

We hypothesize here that age-related social selectivity allows individuals to accrue benefits offered by social ties in ways that mitigate physical and cognitive effects of senescence and the costs of sociality that they amplify. In doing so, we build on past reviews that evaluate

broad patterns of social aging across primates (Machanda and Rosati, 2020), their potential drivers across mammals (Siracusa, Higham et al., 2022), and the characteristics and cognitive-affective components of selectivity in human aging (Carstensen, 2021). Specifically, we focus on defining the phenotype of age-related social selectivity in ways that encompass its potential commonalities in human and non-human primates, and expand on the behavioral and physiological mechanisms that may yield its potential adaptive benefits.

1. Defining age-related social selectivity

The observed social phenotype of age-related selectivity typically consists of two parts: 1) reducing overall social effort and 2) maintaining or increasing effort toward close relationships with a concomitant increase in their quality (Fig. 1A and B). First, individuals decrease social effort with age in the forms of decreased social proximity (from individuals or groups), fewer social partners, decreased time spent in social interactions, and/or decreased attention to social stimuli. These changes are expected to track more closely with physical, physiological, and/or cognitive decline with age rather than with chronological age alone. However, observed declines in sociality do not necessarily mean that animals are pursuing an adaptive social strategy.

The second necessary criterion defining age-related selectivity is that aging individuals modify social effort to sustain or increase effort towards close social partners and among them cultivate higher-quality relationships. Higher-quality relationships are reflected in a more favorable balance of positive and negative social experience, and align with attributes such as greater equitability, stability, improved tenor (Silk et al., 2013), or reported emotional closeness (Carstensen, 2021). In combination with declining social effort, the improvement in close relationships can result in a social tradeoff, where individuals lose peripheral or weaker ties while maintaining or increasing strength of association with close partners. The effects of social selectivity may also be evidenced by social network position. Shrinking ego networks (an individual's direct ties) with sustained or increased indirect connections (e.g., centrality, local transitivity) indicate a selection of partners that are well-connected. For this to occur, aging individuals may have acquired the means to navigate the complexities of their social environment more effectively. For instance, older individuals may benefit from improved knowledge of who the most reliable or valuable social partners are, may reap the benefits of long-term investments in particular partners, or they may have skills and attributes that alter others' behavior towards them. Given any need for familiarity to evaluate individual attributes and behavior, these benefits to older individuals may only be expected with long-term group membership.

2. Evaluating demographic and age-related constraints and confounds

Constraints on sociality are important influences on patterns of social aging that have yet received little research attention in non-human primates (but see Lacreuse et al., 2020 and Negrey et al., 2023). However, we emphasize that they do not necessarily result in social selectivity, for which a selective investment in high-quality partners is necessary. Individuals may have restricted social behavior because of several demographic and physical processes beyond their control. Most obviously, if new relationships are not formed, then existing social partners may be gradually lost through deaths (Hobbs and Burke, 2017). Primates often exhibit preferences for age-matched partners (Ehardt, 1988; Silk et al., 2006), thus older animals seeking out other old animals might naturally focus on fewer partners. Senescence also imposes internal constraints that disrupt individual social effort. For example, musculoskeletal aging can make it more challenging for individuals to keep up with group movements or to travel with social partners (reviewed in Siracusa, Higham et al., 2022). Indeed, limited mobility and increased rates of illness often lead to declines in partner number in

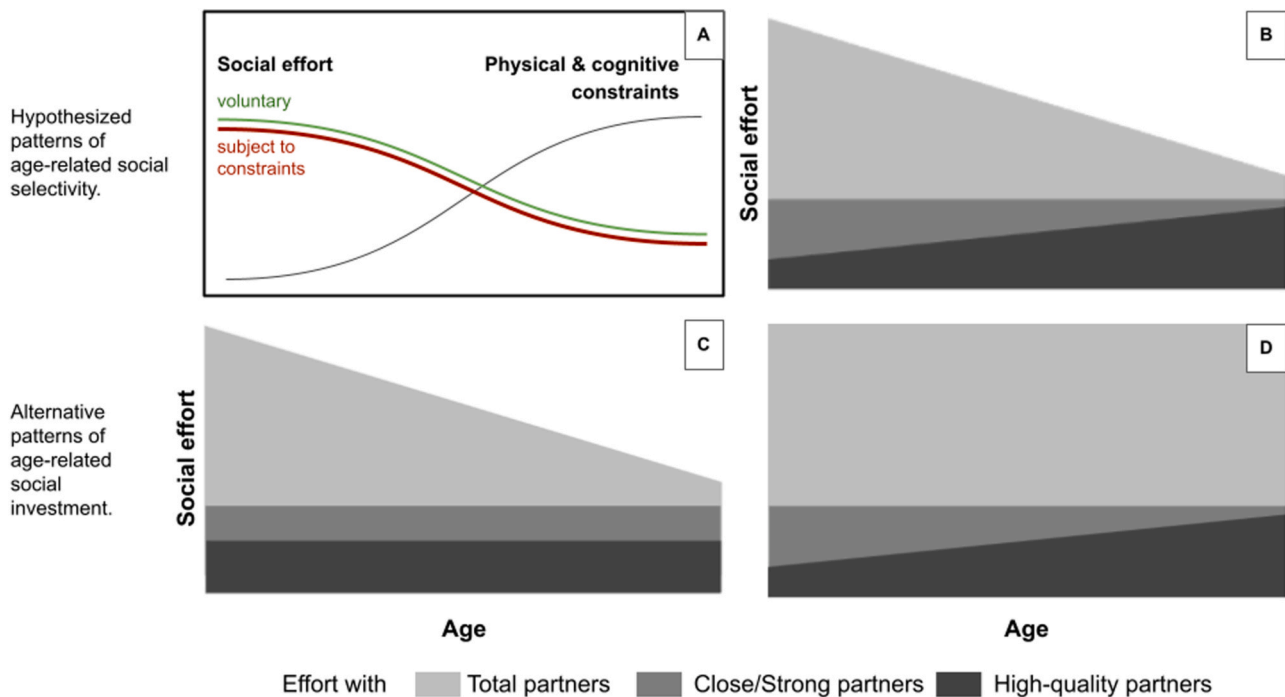


Fig. 1. Example scenarios: varying components of age-related social selectivity and related constraints. Figs. A & B represent a scenario of the age-related social selectivity phenotype observed in humans and certain non-human primates. A) Social effort declines with age in relation to physical and cognitive constraints on sociality. Part of the decline in social effort is involuntary and based on declines in physical and cognitive function necessary for maintaining social contact and relationships. Another part of declining social effort is voluntary, facilitating the second component of social selectivity: B) where individuals focus remaining effort on close partners and increase those that are relatively high quality. Shaded areas represent proportion of total partners in each category. Figs. C & D represent alternative scenarios of social change with age, the health and fitness correlates of which are useful to tease apart the potential benefits of selectivity (A-B). C) Individuals reduce social effort with age to focus on close partners with no corresponding increase in partner quality. D) Individuals do not reduce social effort however increase their focus on high-quality partners by cultivating more of them.

Effort: Number of or time with social partners

Close or strong partners: Partners that individuals identify as important or frequently interact with

High-quality partners: Partners with whom individuals have relationships that are either mutual, more equitable, reciprocal, lower in conflict and/or more supportive.

humans for these reasons (Huxhold et al., 2013; Uchino and Rook, 2020). A confluence of limited mobility and demographic processes may also limit social contact, such as in humans where population decline in rural areas and population mobility lead to greater partner loss with age (Huxhold and Fiori, 2019). Cognitive and sensory constraints of aging may be expected to affect individuals' ability to track and process social information, make decisions, and potentially to see and hear critical social stimuli (Gray and Barnes, 2019; Roth et al., 2004). Finally, in the eyes of social partners, such physical and cognitive limitations of aging can change the competitive ability or social value of older individuals (Hummert, 1990; Reyes-Garcia et al., 2008; Roberts, 2021), making them less attractive as allies or leaders (von Rueden et al., 2014) and contributing to lower social contact. Note, however, that older individuals may in some cases be valuable social partners because of their predictability, social experience, and knowledge or skills (Garfield et al., 2019; Herndon, 2010).

Alternative demographic and age-related processes may confound results to yield patterns that are similar to age-related social selectivity. Mortality selection for individuals with either weaker relationships or more gregarious social phenotypes may result in cross-sectional patterns where older individuals maintain strong ties with few individuals. For this reason, longitudinal data to capture within individual changes are critical. Age-centering is one approach to specifically capture within-individual aging patterns (e.g. Siracusa, Negron-Del Valle et al., 2022) and is particularly valuable in cross-sectional and mixed-longitudinal designs on species with high adult mortality rates. In species that form their strongest ties with close kin, shifts in the availability of such kin over time may underlie changes in partner number and relationship

quality. For example, older females will eventually lose their mothers but may continue to produce daughters, potentially leading females to have more valuable and high-quality social partners with age. Analytically controlling for the number of available close kin with age is one approach to overcome such a confound. Additionally, a correlation between relationship quality and age in early adulthood may emerge as a product of social maturation (e.g., early establishment of stable ties resulting from learning and experience), and this trajectory may be difficult to isolate from social changes in later life that are a particular response to senescence.

3. Evidence for the two parts of age-related social selectivity in non-human primates

Social aging patterns in primates are broadly consistent with the first part of the social selectivity phenotype. That is, most species examined demonstrate reduced social effort among older individuals in mixed-longitudinal and cross-sectional data, characterized by greater social distance from others, fewer social partners, and lower investment in social activity (reviewed in Machanda and Rosati, 2020). Few studies have yet demonstrated evidence consistent with the second part of the definition, which is critical in observational studies to distinguish social selectivity from constrained sociality that occurs as a byproduct of the aging process itself.

Evidence for social selectivity has begun to emerge in a handful of anthropoid primates, including humans' closest living relatives, chimpanzees. Older male chimpanzees have fewer social partners than younger males, but their relationships are more equitable, where

partners have a mutual preference and grooming is well-reciprocated (Rosati et al., 2020). Older males retain a central position in the affiliative social network, despite declining rank and fewer direct ties (Thompson González et al., 2021). Older male chimpanzees also make efficient use of social opportunities. They spend less time in social groups, which may result from aging constraints, but when they join groups, they spend more time in close proximity to social partners (Rosati et al., 2020). Changes in social status and availability of kin partners do not explain these patterns.

Evidence of social selectivity also comes from the macaques. Adult female rhesus macaques had fewer social partners as they age (grooming and proximity) but maintained overall levels of social engagement, and had a greater proportion of kin among close partners, suggesting selective investment in valuable relationships (Siracusa, Negron-Del Valle et al., 2022). This finding was not attributable to loss of partners by death. Older adult females were also more likely to be social partners with individuals that they had strong relationships within previous years. In closely related Barbary macaques, both males and females exhibit lower social effort at older ages, paralleling lower physical function and exploratory motivation (Almeling et al., 2016; Rathke and Fischer, 2021). Experimental evidence further demonstrates that Barbary females remain interested in social stimuli as they age and that both younger and older females attend to stimuli from a close contact more strongly than from a non-contact (Almeling et al., 2016). Thus, it remains unclear whether female Barbary macaques are demonstrating the second criterion, i.e. a greater focus of effort on close relationships of relatively higher quality.

4. Proximate causes of age-related selectivity: Socioemotional selectivity

In humans, social selectivity is driven in part by shifts in emotional goals and motivational priorities that moderate investment in higher quality relationships. This is characterized by a “positivity effect”, wherein older individuals are more attentive to positive vs. negative social stimuli and as a result prioritize positive social interactions (Carstensen and DeLiema, 2018; Charles et al., 2009; Charles and Carstensen, 2010; Luong et al., 2011). Senescence-related constraints do not themselves appear to shape a motivation to engage in more positive and higher quality relationships. A positivity effect does not result from neural or cognitive decline wherein, for example, negative information may become more difficult to process and thus more aversive (Carstensen and DeLiema, 2018). Instead, people with preserved rather than degraded cognitive function during aging are more likely to orient toward positive emotional information (Kalenzaga et al., 2016). Similarly, older adults with greater connectivity between the amygdala and medial prefrontal cortex show greater memory for faces expressing positive vs. negative emotions (Sakaki et al., 2013). Because the relationships between neurocognitive health and positivity are present in older but not younger individuals, these findings are interpreted to suggest that the emergence of the positivity effect with age is the non-pathological, and potentially adaptive, fading of a bias toward negative stimuli at younger ages (Carstensen and DeLiema, 2018). Thus, the emotional and behavioral mechanisms involved in positivity biases may constitute a third component of age-related social selectivity.

A similar positivity bias occurs in concert with social selectivity in male chimpanzees, who engage in fewer bouts of aggression and a higher proportion of positive versus negative social interactions as they age (Rosati et al., 2020). Thus, it is possible that social selectivity in chimpanzees involves human-like socioemotional mechanisms. In contrast, many primates appear to exhibit a pattern of negativity bias with age, including lower rates of grooming with age that lead to a predominance of negative social interactions (Machanda and Rosati, 2020). It is not yet clear how widespread a positivity effect is among primates, whether it is consistently linked to socially selective aging strategies, or whether positivity biases drive or result from social aging

strategies. Notably, the phenomenon of socioemotional selectivity, wherein emotional mechanisms regulate social preferences, is distinct from “socioemotional selectivity theory” (Carstensen, 2021), which posits that cognitive processing of time horizons serves as a mechanism to shift emotional goals and drive a positivity effect.

5. Potential adaptive advantages of age-related social selectivity

Historically, psychological and sociological theories of human social aging have focused on cognitive and social environmental mechanisms to explain greater social selectivity at later ages, however, they have not necessarily invoked biological adaptation. Life-span psychological theories, such as Selection, Optimization, and Compensation (Baltes and Goulet, 1970; Baltes and Baltes, 1990; Freund, 2008) and Socioemotional Selectivity (Carstensen et al., 1999), posit that perceived availability of resources, including time, alter personal and interpersonal goals and related priorities over the life course. For example, people who perceive that they have less time to live, even when this perception is due to experimental stimuli, exhibit altered social priorities, including greater prioritization of emotional well-being (reviewed in Carstensen, 2021). The Social Convoy model, in contrast, emphasizes that life events, such as retirement or widowhood, act as proximate catalysts for declining number of partners at later ages (Fuller et al., 2020; Wrzus et al., 2013).

We find the evidence for age-related social selectivity in at least some non-humans a compelling reason to inquire whether the complex cognitive and emotional mechanisms in humans overlay an adaptive response inherited from our evolutionary ancestors. That is, aging individuals may make the best of a bad job by reducing aspects of social effort and prioritizing valuable relationships as a means to ameliorate the fitness-limiting constraints of cognitive and physical senescence. If so, emotional and cognitive mechanisms may be an important way to regulate social priorities as humans age, but we expect to see that these priorities allow aging individuals to achieve some improved ‘efficiency’ of social investment, as above, and ultimately reap some residual fitness advantages during the later years of life. Notably, the pattern of social selectivity in aging chimpanzee males is associated with an unusually long period of effective breeding compared to many other primates (Muller et al., 2020), while prioritization of valued partners in aging humans could generate adaptive advantages if it were an effective strategy to promote inclusive fitness (e.g., Herndon, 2010; Kaplan et al., 2000; Kim et al., 2012, 2014) or for aging men to gain direct reproductive advantages of age-based prestige (e.g., Marlowe, 2000; Tuljapourkar et al., 2007).

A selective focus on close and higher quality ties likely yields benefits that are not exclusive to old age, but which may be particularly important given the physical challenges of senescence and individuals’ loss of competitive ability. For example, focusing friendly interactions towards close partners is a strategy to cope with external threats throughout adulthood for female baboons (e.g., Crockford et al., 2008; Wittig et al., 2008). However, such a focus may be particularly advantageous in older individuals that experience ongoing functional decline, increased likelihood of partner loss and bereavement, and increased sensitivity to adverse events (Kiecolt-Glaser and Glaser, 2001; Uchino and Rook, 2020). Older individuals may also be less likely to suffer the opportunity costs of eschewing many diverse relationships, as these may be specifically beneficial early in life for gaining information and rising in status (McDonald, 2007; Wrzus et al., 2013).

6. Key potential mechanisms of adaptive benefits

We expect that several of the adaptive benefits of age-related social selectivity involve 1) enhancing reproductive success and/or inclusive fitness and 2) the extension of lifespan and/or healthspan, the period of life in which individuals are free from either chronic disease or severe disability. These adaptive benefits of social selectivity are not mutually

exclusive: although health and fitness are distinct outcomes, behavior that extends healthspan is likely to be adaptive. For example, evolutionary theories on the extension of lifespan in humans frequently point to the inclusive fitness gained by older individuals in rendering cooperative aid to younger relatives through activities like foraging and childcare that require continued physical and cognitive vigor (Herndon, 2010; Kaplan et al., 2000). Non-human primates that form strong support networks with kin may similarly derive inclusive fitness benefits from prolonged periods of the lifespan in good health. Pathways from social ties to health and fitness are complex, and a holistic perspective on them extends from behavioral (e.g., cooperation) to physiological (e.g., immune regulation) mechanisms.

At the behavioral level, focusing social effort toward more positive and mutual partners may enhance reproductive success. As individuals age, the loss of physical strength constrains behavior associated with reproductive success, such as aggression. Males, in particular, may compensate for this physical susceptibility and lack of aggression by forming associations with others and engaging in coalitions or cooperative mate guarding when females are sexually receptive. In fact, in chimpanzees and Barbary macaques, a larger proportion of aggression in older males is coalitionary (Muller et al., 2019; Rathke et al., 2017). An equitable exchange of grooming among older male chimpanzees' partners may facilitate such cooperation, as coalitionary support is reciprocated in a similar fashion and in exchange for grooming (Watts, 2002). Efficient use of such allies may also explain the ability of male chimpanzees to extend their reproductive careers long past their physical prime (Muller et al., 2020). Women and females also appear to target investment in individuals that maximize reproductive success, however through kin selection and grandmothering. In studies from European populations, older women are more likely than men to maintain contact with individuals from multiple generations and focus interaction on family and close kin (Bhattacharya et al., 2016; David-Barrett et al., 2016). Such patterns are also evident in rhesus macaques, where kin make up a larger proportion of close partners for older vs. younger females (Siracusa, Negron-Del Valle et al., 2022). Although both sexes become more socially selective with age in humans (Antonucci et al., 2014; Antonucci and Akiyama, 1987), it appears that older males and females target investment in different types of partners in line with their different reproductive strategies.

The tendency toward cooperation and tolerance within close relationships leads to other direct fitness benefits, such as protection from adverse experiences that raise the risk of injury and subsequent illness (Cohen and Wills, 1985; Thompson, 2019). Cooperative support and security are often intertwined such that close relationships assist in the avoidance of predators (Micheletta et al., 2012), prevention of harassment (Cameron et al., 2009; Stanton and Mann, 2012), and protection from extreme cold (McFarland et al., 2015; McFarland and Majolo, 2013). Avoiding each of these risks may be critical in old age, as individuals are likely to have reduced sensory perception, immune function, and thermoregulatory capacity (Gosain and DiPietro, 2004; Siracusa et al., 2022).

On a physiological level, at least three mechanisms may allow social selectivity to improve health at older ages via the cooperative and positive local environment that it creates: improved HPA axis regulation, improved immune regulation, and decelerated cognitive decline. Aging is associated with dysregulation of the HPA axis and increased exposure to glucocorticoids (chimpanzees, Emery Thompson et al., 2020a; humans, Gaffey et al., 2016; baboons, Sapolsky and Altmann, 1991), which exacerbates links between stress and aging pathologies (Cohen et al., 2012; Sapolsky et al., 2002). Friendly social contact typically lowers and buffers HPA activity in social animals, enabling faster returns to baseline from acute elevations in activity (Kikusui et al., 2006; Wittig et al., 2008, 2016). Supportive ties do this in part via the anxiolytic effects of the oxytocin that exposure to close partners releases (Carter, 2014) and by altering psychological processing of the stressor itself (Sapolsky, 2011). Social contact focused on a smaller set of

partners, in particular, enhances this buffering effect (Crockford et al., 2008; Wittig et al., 2008). For example, adult female baboons decreased their partner numbers and focused grooming to close social partners during the threat of infanticide, and the more a female decreased, the faster her stress response returned to baseline (Wittig et al., 2008). This suggests that social strategies that allow older individuals to benefit from improved buffering and HPA regulation while avoiding social risk could contribute to a range of improved health outcomes, including reduced risk of inflammation, hypertension, and other cardiovascular disease (Cohen et al., 2012; Gaffey et al., 2016).

A related physiological pathway affected by the social environment is immune regulation. The dysregulation of the immune system is a prominent feature of biological aging that is shaped both by chronological age and socio-environmental experiences. The general decline in adaptive immune function that characterizes immunosenescence (Aw et al., 2007; Gruver et al., 2007) and the increase in innate inflammation that characterizes inflammaging (Franceschi et al., 2018; Reed, 2019), closely parallel the outcomes of the influence of social status on immunity in animal models (Bartolomucci, 2007; W. Lee et al., 2022; Snyder-Mackler et al., 2016; Tung et al., 2012). The influences of social status on immune profiles appear to be mediated via the direct experiences of higher and lower status individuals, such as rates of friendly behavior and aggression, and their influences on the HPA axis (Anderson et al., 2022; Snyder-Mackler et al., 2016; Tung et al., 2012). In rhesus macaques and baboons, higher-ranking females that had more positive and less negative social interactions maintained immune profiles that were more aligned with youth, such as higher investment in adaptive immunity and lower inflammation (Anderson et al., 2022; Snyder-Mackler et al., 2016). Social selectivity during aging could allow individuals to experience such socially-derived benefits of immune regulation, while avoiding the risks of disease exposure and injury from associating with many partners of various quality.

Although the effects of social stress and aging on immunity are similar, there is also more direct evidence that social stress can accelerate immunological aging. In humans, chronic social and psychological stress can amplify the age-related imbalance of naive to memory T cells (Aiello et al., 2016), shorten leukocyte telomeres (Gebreab et al., 2016), and impair already lowered responses to vaccines (Glaser and Kiecolt-Glaser, 2005). Further, social stress exacerbates age-related inflammation, including accelerated secretion of inflammatory cytokines (Casaletto et al., 2018) and higher c-reactive protein after a 15-year follow up (Herriot et al., 2017). In contrast, the positivity effect of socioemotional selectivity appears to play a role in healthy immune aging, as individuals with greater positive recall had higher T helper cell counts and lower T helper cell activation 1 and 2 years later (Kalokerinos et al., 2014).

An additional physiological pathway by which social selectivity may influence health and fitness is improved cognitive aging. A rich body of literature demonstrates that social engagement is a key factor in cognitive function at older ages in humans (Stine-Morrow and Manabasi, 2022), such that greater engagement corresponds with slower declines (James et al., 2011; Pugh et al., 2021) and relatively higher function in an array of cognitive domains (Barnes et al., 2007; Boss et al., 2015, p. 201; Small et al., 2012; Tilvis et al., 2004). Evidence also suggests that engagement with fewer, close partners may provide neuroprotective benefits. Among older African Americans, having more social partners was associated with declines in processing speed over time, however greater social engagement was associated with slower declines in the majority of cognitive domains evaluated (Pugh et al., 2021). In addition, increases in emotional support, rather than instrumental support, correspond with increases in cognitive function (Ellwardt et al., 2013), suggesting that the most beneficial support may be found in higher quality relationships rather than transactional exchanges. Indeed, higher satisfaction with social partners and perceived reciprocity was associated with a 23% and 53% reduction in dementia risk, respectively, in a 15-year follow up study of a French cohort

(Amieva et al., 2010). Beyond the cognitive stimulation of positive social engagement, one suggested biological pathway from engagement to cognitive health involves decreased neuro-inflammation (Dause and Kirby, 2019). This emphasizes that the three biological mechanisms of increased healthspan herein outlined are likely to be highly intertwined. Although evidence of cognitive decline with age is still emerging from non-human primates (see previous citations), this mechanism of selectivity's adaptive benefits would be valuable to explore in greater phylogenetic breadth.

7. Approaches for further research

Substantial evidence suggests that strong and supportive social ties are beneficial in old age for humans (English and Carstensen, 2014; Fuller-Iglesias, 2015; Fung et al., 2001; Shah et al., 2023), however the link between the degree of selectivity per se and health and fitness in humans and across primates is less certain. Future research can examine how the different components of selectivity, i.e., declines in social effort and increases in partner quality (Fig. 1A and B), interact or synergize in particular circumstances to yield adaptive benefits during aging. For example, in the face of shrinking numbers of social partners, are individuals that improve partner quality (Fig. 1B) at a greater advantage than those that do not (Fig. 1C)? One would predict yes, particularly if declines result primarily from age-related constraints such that individuals are in poor condition.

Another question is whether reducing partners to close relationships (Fig. 1B or C) is any more or less advantageous than simply increasing the quality of close relationships (Fig. 1D). Among Germans aged 40–85 years, greater emotional support and engagement at time 1 was associated with better functional health at time 2, regardless of any decrease in partners (Huxhold et al., 2013). Similarly, in studies in the United States and Portugal, having emotionally close ties was more important than number of partners for improving quality of life and emotional well-being in old age (English and Carstensen, 2014; Gouveia et al., 2016). These studies suggest that cultivating and receiving emotional support is a primary influence on health and wellness, however modifying social effort and partner number are not. Alternatively, research in the cognitive domain suggests that maintaining many social partners in old age may be deleterious (Pugh et al., 2021). Such findings suggest that older individuals may indeed optimally combine reduced social effort with selectively improved quality of social relationships (Fig. 1B).

It becomes clear that the occurrence and benefits of social selectivity will likely depend on individual condition, including their physical, cognitive, and social reserves. This falls in line with Selection, Optimization, and Compensation theory (Baltes and Baltes, 1990; Freund, 2008) where the need for selectivity at older ages stems from a lack of resources. Such reserves may be proxied by current social status or previous life experience. For example, high social engagement earlier in life appears to build a cognitive reserve in hippocampal function (Dause Kirby, 2018). Further, in chimpanzees and rhesus macaques, social status influences age-related changes in sociality. Regardless of age, high ranking male chimpanzees receive grooming from more partners (Thompson González et al., 2021), are more often present and in close proximity with other males, and maintain more mutually positive relationships (Rosati et al., 2020). In rhesus, higher ranking female rhesus show shallower declines with age in the number of partners that they approach (Siracusa, Negrón-Del Valle et al., 2022). Following this reserves hypothesis, older individuals with high social, physical, and cognitive reserves may be expected to show a weaker signal of selectivity, as they maintain a relatively large number of social partners consisting of high-quality relationships (e.g., Fig. 1D). In tandem, old and lower status individuals may be more likely to withdraw socially and focus on trusted partners to avoid status-related aggression (Fig. 1B or C). Alternatively, selectivity may be difficult to identify in high status individuals if greater reserves lead to overall declines in social engagement with age. Given abundant resources and good physical condition,

it is possible that little additional value is gained from the cooperation and protection of close and positive relationships.

We propose that the full suite of selectivity (Fig. 1B), and its potential benefits, may be most likely to occur in individuals with declining physical and cognitive ability and who stand to benefit from social ties. Indeed, older people that suffered chronic illness were more likely to reduce their partners to supportive ones with more frequent contact than were people in good health (Lang and Tesch-Römer, 1993). Whether compromised individuals can focus on and maintain high quality relationships will likely lead to the largest measurable differences in health and fitness outcomes.

These approaches to examine the social selectivity phenotype are of direct importance to the health of older adults globally. The United Nations World Population Prospects (2022) projects that individuals > 60 years of age will triple globally by the end of this century, and even more in low and middle income countries. While this will lead to a larger population of elders to care for, it may also change their social dynamics. A firm understanding of social aging will be necessary to meet their needs. Determining which aspects of social selectivity per se represent age-related constraints vs. adaptive strategies will be foundational in advancing older adult care. The effectiveness of policies and interventions to maintain or increase social support and mitigate isolation will likely depend on individuals' condition and context. We expect that research on social selectivity, and social aging broadly, across the diversity of social systems and ecologies among nonhuman primates (e.g., Fischer, 2023; Machanda and Rosati, 2020; Siracusa, Higham et al., 2022) will facilitate insights on social patterns and advantageous strategies relevant to diverse human conditions.

8. Summary

In this review, we characterize the behavioral phenotype of age-related social selectivity and propose pathways by which it may serve as an adaptive strategy. Selectivity is commonly observed in humans and has begun to be increasingly evident in non-human primates, strongly suggesting it evolved as a strategy to cope with the unique costs and constraints on social interaction in old age. Selectivity is typically characterized by an age-related decrease in total number of social partners, or time spent in social engagement, and an increase in positive and high-quality relationships among close partners. This second criterion is necessary to distinguish selectivity from age-related constraints on social interaction; nevertheless, it is not sufficient. Research should carefully examine the role of cognitive and physical constraints in limiting sociality and access to particular social partners, e.g., limited ability to travel. As an adaptive strategy, a focus on positive relationships in old age may provide both behavioral and physiological advantages in the face of diminished physical and cognitive abilities. At a behavioral level, selectivity may facilitate cooperative alliances to achieve reproductive goals and protect against external threats, despite decreases in status and/or physical ability. At a physiological level, such relationships may enhance HPA and immune regulation, and decelerate cognitive decline. Future research will be valuable to characterize the constrained or adaptive nature of each component in the social selectivity phenotype and its potential benefits relative to individual condition.

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