



Aging in Non-Human Primate Society: What Relevance for Social Gerontology?

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Abstract

Wild animals were once thought not to age, as their deaths were viewed as the consequences of constant exposure to the perennial risks of nature. Studies of non-human aging were largely confined to biological investigations, focusing upon short-lived species such as fruit flies, mice and nematodes. Over recent decades, this has changed, and studies of non-human aging have begun to investigate aging taking place in social contexts. The present paper reviews such work on social aging in non-human primate societies. Four themes were evident in seeking potential parallels between human and non-human social aging. These were social disengagement, social bonds or social capital, status rank and dominance, and kinship ties. No studies were found that had explored parent caregiving. The lack of clear evidence that agedness is perceived and recognised within non-human primate groups suggests that most age-associated behavioral changes are at best demi-regularities that map quite imprecisely upon social aging in human societies. However as non-human primate societies are becoming gradually confined to areas and environments established through human agency and human institutions, it is possible to speculate that non-human primate old age will become more common if less natural and as a result, perhaps more akin to social aging in human societies.

Keywords: Non-human Primates; Kinship; Social aging; Social bonds; Social disengagement; Rank and Status

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Aging in Non-Human Primate Society: What Relevance for Social Gerontology?

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Introduction

For quite some time it was thought that aging was rarely observed ‘in the wild.’ Death among wild animals was considered to be largely a random affair, arising from the ever-present dangers posed by the environment, with aging having little opportunity to impose itself as a distinct process on these ‘natural’ patterns of mortality (Gaillard and LeMaitre 2020, 8). Aging was thus considered a phenomenon observed most clearly in human society, since only human societies were able to establish and sustain the kinds of environment securing their members reach old age (Caspari and Lee 2004). In recent decades, the presence and nature of aging ‘in the wild’ has become more evident. Studies have begun to examine in more detail the nature of aging in non-human mammals, and the potential interaction between their aging and their social environment. Traditionally, research on aging in non-human species has employed short-lived laboratory animals such as fruit flies, mice, and nematode worms to study biological variation in lifespan with scant attention to any social aspects of their environment. Given the longer lives of most mammals, studies of their aging and longevity have been more limited, even among non-human mammals living in captivity (Colman 2018). As research into later life in non-human societies has developed in recent decades, it has begun to offer some interesting insights into actuarial aging and – the focus of the present paper – on ‘social aging.’ While much of this focus on social aging can be dated back to the earlier work of Jane Goodall and Sarah Blaffer Hrdy and their studies of apes (Goodall 1986a, 1986b) and monkeys (Hrdy 1981) it is only in the last quarter century that a non-human primate gerontology can be seen emerging.

Research into human aging has shown how the biological features of aging – notably patterns of morbidity and mortality over the life course – vary quite considerably from one period to another, from one society to another, and between social strata within a single society (Sokolovsky 2009). While it is not clear exactly how society ‘gets under the skin’ to achieve such effects, it seems clear enough that it does (Das 2013; Ferraro and Shippee 2009; Green and Darity 2010; Hertzman and Boyce 2010; Taylor, Repetti, and Seeman 1997). Given the powerful impact of social change in human society, exploration of social attributes contributing to human aging and longevity has assumed that it is the distinctive social, economic and cultural development of human society, and especially its progressive modernization, that has had the most powerful effect on shaping human aging. The increase in assets, capital, culture and technology, the strengthening of the social contract and the accumulation of resources evident in the world’s more advanced economies have clearly influenced both the trajectory and the rate of human aging – that is, the timing of its onset, the rate at which it proceeds and the degree of its associated decline (Crimmins 2020). How far might it be possible to identify similar effects (i.e., social effects on the onset, degree and speed of aging) in non-human societies? In the absence of any direct equivalence between developments in human society and the relative stability of non-human social species, is there evidence of social aging in non-human societies?

Although the potential of cross-species comparisons for informing the study of social aging was noted some time ago (Pavelka 1994) such endeavours have had only a very limited impact on either contemporary age studies, the sociology of aging or social gerontology. Primate anthropologist, Mary Pavelka, was herself rather skeptical that age and aging were significant aspects of non-human society (Pavelka 1990, 372). Since then, there have been significant developments. This paper is intended to examine systematically whether social aging is a meaningful concept in non-human societies, and if so, whether any substantive benefit can be gained from integrating research into social aging in non-human societies with that in human society. In choosing to examine this question, my focus here is specifically upon primates as the genera to which human beings belong and which share our “long slow life histories” (Jones 2011). Unlike most other mammals, primates “grow more slowly, have later ages at first reproduction, live longer lifespans and lower fertility” (Jones 2011, R708). Given the common experience of a long adult life spent in the context of social groups, it seems reasonable to assume that the impact of such conditions might be more conducive to identifying potential commonalities in social aging. Hence, rather than review aging across the large and diverse class of mammals, as some have done in relation to social aging (e.g., Siracusa et al. 2022), this review is confined strictly to studies of apes and monkeys whose aging was first drawn attention to by the works of Jane Goodall and Sara Blaffer Hrdy (Goodall 1986a; Hrdy 1981). Even here, of course, considerable variability exists between species and between habitats.¹

Identifying Common Research Themes in Social Aging

Animal models have been used frequently to explore commonalities and differences in behavioral and biological processes between human and non-human mammals. Fewer attempts have been made to study how social behavior and social organization in non-human mammals might illuminate human social aging, whether through their commonalities or, equally importantly, by their differences. Focusing upon the primate literature published over the last three decades, four distinct social aging themes can be identified.² First are the several studies which focus upon what might be called ‘animal models’ of late life social disengagement (e.g., Corr 2003; Fischer 2017; Machanda and Rosati 2020). One recent review of this area, for example, concluded that, at least among female monkeys, there is evidence of their disengagement with age, in the form of reduced social interests, restricted social contacts, and less exploration of the environment (Fischer 2017). The second theme concerns the value of social bonds in maintaining health and well-being in later life. Here the emphasis has been on assessing the size and strength of social bonds and how far they increase fitness and survival among older non-human primates (Ellis et al. 2019). Such research reveals how much the particular species and the particular measures for assessing sociality vary in their contribution to survivor benefit in later life. The third theme concerns the relationship between age, rank, and status, and the patterns of dominance that can be observed between younger and older adult non-human primates (e.g., Borries, Sommer, and Srivastava 1991; Macmillan, 1989). In this context, status is typically measured by evidence of the relative dominance (versus yielding) of individual group members in their encounters with other members of the group (Drews 1993).³ The fourth theme concerns the impact of kinship ties on members’ aging, health, and longevity. One frequently explored topic has been the so-called ‘grandmother hypothesis,’ namely the notion that by enacting family caregiving roles, older, post-reproductive adults promote both their own health and survivorship, as well as the well-being of the young of the species (Kim, Coxworth, and Hawkes 2012; Peccei 2001). The existence of a significant post-reproductive period in the life course, most sharply evidenced by the human menopause, but linked with the more gradual loss of fertility in many primate species is thought to increase the capacity of adult children to raise, look after, and sustain their own children, and thus promote the family gene pool, while also being of benefit to the grandparents themselves (Kim, Coxworth, and Hawkes 2012; Pavelka, Fedigan and, Zohar, 2002; Peccei 2001). Other themes have appeared in the literature, notably responses to death and

dying within primate society, which though linked, can be considered a distinct topic in themselves, and which have been quite fully reviewed elsewhere (Gonçalves and Carvalho 2019). Some themes are notable by their absence, not least studies examining patterns of care shown toward the oldest old in primate society. Anecdotal observations however suggest that “[u]nlike humans, non-human primates do not receive substantial support from group-mates if their physical condition compromises foraging” (Thompson González et al. 2020, 2).

In the main part of this paper, each of these four social themes – social disengagement, social capital, social status, and inter-generational kinship – will be elaborated, citing research primarily as illustration of how these kinds of themes might be linked with human social aging. As noted, this review does not aim to offer an exhaustive account of all published studies on non-human primates. The intent is to illustrate the potential – and limitations – of these research findings on aging in non-human primate societies, as well as highlighting the pitfalls in their ‘translation’ to aging in human society. Before addressing these four themes a preliminary, but important consideration needs to be made, namely how far ‘age’ and ‘agedness’ are recognized in non-human primate societies, and whether, once adulthood/sexual maturity has been reached, further age or life stages can be distinguished as meaningful social realities for such groups. Since this question is critical in assessing how aging in these settings might best be realized as a social phenomenon, it will be addressed first.

Age Recognition in Non-Human Primate Society

How far does agedness serve as a stimulus for social behavior in non-human societies? While there exists a considerable literature in aging studies and social gerontology on the perception of and judgements about age and agedness, such studies are presaged upon a widespread recognition of agedness, both as a social status and as a (perceptible) physical identity. Hence the study of age discrimination, attitudes toward old people and ageism constitute major topics in these fields (North and Fiske 2015). How distinct is the physical appearance of age among non-human primates and how evident are observable aged behaviors among such primate groups? If, for example, there is little evidence that non-human primates can and do distinguish between old and mature conspecifics, one might expect that social behavior and social bonds directed toward older adult conspecifics by other adults would not be evident. If indeed there are age changes in sociability however, arising from intrinsic aging processes, might such behavioral changes (rather than any other markers of age) serve instead as the stimulus affecting others’ behavior? If such is the case, might ‘aging’ behaviors be rather less aligned to both chronology and the appearance of age, contrary to reactions to the appearance of age evident in human society.

While facial recognition is well developed in primates, and most primates can distinguish between familiar and unfamiliar conspecifics, the development of individual recognition might occur independently of any higher order recognition of classes or categories beyond, say, familiar versus unfamiliar or kin versus non-kin (Tibbetts and Dale 2007). To address this question of age-recognition, I will focus first upon what evidence there is of age-embodied physical changes in the appearance of non-human primates, before turning to evidence of behavioral changes associated with older age. The physical signs of age in non-human mammals have rarely been commented on by human researchers, in part, it would seem, because few reliable ways of ascertaining agedness have been established (Dagg 2009). While most mammals do show visible signs of agedness, like loss of fur, hair, and muscle mass as well as evident slowness of movement, these are by no means reliable indicators of chronological age (Lowenstine, McManamon, and Terio 2016). No system has yet been developed that categorizes observable post-adult changes in appearance and correlated them with animals’ known chronological ages. While classificatory systems do exist, they either emphasize early developmental stages, which

stop once mature adulthood is reached (e.g., Garber et al. 2020; Turner, Anapol, and Jolly 1997) or they constitute post-hoc categorisations based entirely upon either known chronological age or post-mortem cranial and dental analyses (cf. Schultz 2004, 85). In general, the use of either behavioral or observational methods of age classification beyond adulthood “can lead to contradictory conclusions” (Balcells and Baro 2009, 7).

It is perhaps no surprise then that initial attempts to categorize the later stages of life and to provide estimates of primate longevity have had to be consistently revised upwards (Washburn 1982, 15-17). Put succinctly, it seems difficult for us as human beings to readily distinguish between non-human primate stages of maturity and late adulthood. Research employing age as a key variable, therefore, has typically been conducted on captive populations where apes have been raised and maintained as lab animals from a reasonably early age, with fairly accurate knowledge of their ages arising from the detailed records of their time at the research center (Tarou et al. 2002, 212). Whether their conspecifics share with their human researchers this problem of not being able to differentiate post-adult life stages is a question largely unresearched but it is clear that chronological age *per se* has little if any social meaning within non-human primate societies.

Still, there is some evidence that age group distinctions can be and are made – at least in terms of patterns of age-differentiated social behavior. Albon Lemasson and colleagues (2010) found that older monkeys elicited more responses from their younger conspecifics despite emitting fewer calls themselves. Similar findings were reported in a community of marmosets (Chen, Kaplan, and Rogers 2009). Other studies have indicated that there are characteristic changes in the vocalization of some primates, such that older adult Japanese monkeys elicit more harsh syllables in their food calls than do younger adults (Inoue 1988). Whether perceptual discrimination of age by conspecifics – by sight, sound, or other senses – is demonstrable, however, is not clear. Evidence of visual discrimination of agedness among non-human primates is limited, with most studies focusing upon distinctions made between infants and adults, rather than between mature and old adults (Sato et al. 2012).

In sum, given the difficulty in identifying reliable physical markers of agedness in most primates, there remains considerable doubt whether non-human primates show evidence of adult age discrimination – and hence any non-human equivalence to ageism or age prejudice. While there is evidence that some behaviors of older adult primates can be distinguished – by researchers – from those of younger adults, and that some differential behaviors can be discerned that are directed toward older adults by younger adults, this shows only that behavioral changes associated with age are socially realized within non-human primate social groups, not that this constitutes some form of prejudice, special affection for, or deliberate avoidance of older conspecifics. Whether this represents anything more significant than changing response behavior to changing stimulus behavior, however, is difficult to ascertain. More deliberate experimentation, such as that intended to demonstrate differential responses to infants, has not been carried out and arguably even if it were it would still provide little evidence of preference for or against older adult primates. Age discrimination as a perceptual frame among non-human primates however has not been shown and seems somewhat unlikely and certainly less pervasive than is found in human society.

Aging and Social Disengagement

Studies of aging in human societies have provided consistent evidence of changes in social behavior and network size with age such that most people’s social networks decline during adulthood, except for family (kin) networks (Wrzus et al. 2013). From such observations, two important theoretical propositions have been developed. The first is *Disengagement Theory* (Cumming et al. 1960); the second

is *Socioemotional Selectivity Theory* (Carstensen, Isaacowitz, and Charles 1999). While the former assumes that, with age, individuals withdraw from the wider society, the latter postulates that this withdrawal affects mostly non-intimate social connections, while emotionally close relations are maintained into and through later life. These theoretical formulations have guided several studies of non-human primates designed to see whether these human patterns of social interaction fit age-associated changes in sociality among non-human primates.

Mary Pavelka has argued against drawing too close comparisons between age related changes in sociality among human and non-human primates (Pavelka 1991). She argues that at least three distinctly human features of later life set human social aging apart from that of non-human primates, namely the universality of menopause in human beings, the age-associated division of labor whereby younger adults engage more in production and older adults in consumption, and the significant human awareness of aging and mortality. Given these considerations, Pavelka argues that there is little reason to “expect there to be a social category for the elderly” for monkeys (1991, 396). She further argues that “frailty to the point of dependence is not a characteristic of old monkeys or old apes because animals in this position would simply die” (Ibid, 396).

Other studies, however, have found evidence of age-associated social disengagement both in monkeys and in apes. Primatologists Gabriele Schino and Marta Pinzaglia (2019), for example, studied the social behavior of a colony of capuchin monkeys and found that, with age, affiliative interactions decreased, with older monkeys engaging in less mutual grooming and spent less time in proximity with other adult conspecifics. They observed what they described as an increased tendency to select preferred partners to engage in grooming. They posited this reflected one of the tenets of socioemotional selectivity, as outlined by Laura Carstensen and her colleagues (1999), namely that with age, social contacts became both narrower and more exclusive (Schino and Pinzaglia 2019, 5). Their conclusion supports Pavelka’s contention that the phenomena of increasing socioemotional selectivity with increasing age may be “taxonomically widespread” and not dependent upon the advanced cognitive abilities by which humans are aware of their own future lifetime (Schino and Pinzaglia 2018, 6).

These effects seem if anything more pronounced in apes. Nicole Thompson González and colleagues (2021) observed declines in social engagement with age among both male and female chimpanzees, but with what these authors called increasing “cliquishness” among the older males. Despite a reduction in their overall social contacts (reflected for example by the amount of grooming), these authors observed that among those who continued to groom and be groomed, there was a tendency for this to be increasingly confined to a small group (“clique”) (Thompson González et al. 2021). This social selectivity was evident in Siracusa and colleagues’ (2022) longitudinal study of female rhesus monkeys when they observed a narrowing of the monkeys’ social networks with age over an eight-year period. These results were not the consequence of any absolute reduction in the total amount of social behavior with age nor were they the consequence of the deaths of social partners.

Such studies imply that across most non-human primate groups there is a narrowing of social relations and, particularly among the great apes, a degree of intensification of those relations despite an overall decline in social activities. Rather than complete social disengagement, there is evidence of selective disengagement compared with earlier social relations – with older males being less gregarious but maintaining their close friendships well into later life (Rosati et al. 2020). Since such effects have been observed in both genders and in wild and captive populations, there seems strong support for some form of social aging across the primates, albeit one characterized less by signs of disengagement but rather increasing social selectivity. What this suggests is that social embeddedness retains its

importance for primates in later life every bit as much as earlier in life even if the form of that embeddedness changes with age.

Aging and Social Capital

Using the term ‘social capital’ to refer to the size and strength of social ties, research in non-human primates has generally concluded that primates with greater amounts of social capital more often thrive than those lacking in social capital (Silk et al. 2010). In recording levels of social capital in female baboons, Silk and colleagues used two composite measures: one reflecting social dominance (based on the ratio of *approach* to versus *retreat from* other females in the group) and the other reflecting relationship quality (a composite of the stability of the social ties and their strength, as measured by the frequency and duration of grooming). The authors found that both indices contributed to greater longevity and reinforced the value of social capital as a source of variation in adult fitness and survival in non-human primates. It may however be worth distinguishing between these two forms – namely sociability and dominance/status. For the purposes of this section of the paper, the review of social capital will be confined to studies of social contacts, defined by the degree of their engagement and valence, to use Zarin Machanda and Alexandra Rosati’s terms (2020, 2). This means that questions of dominance, rank, and status will be ignored until the next section.

Some researchers have argued that despite a decline in the size of social networks with age, the ‘healthy aging’ benefit of sociality applies less to older adults than it does to early or mid-age adult primates (Brent, Ruiz-Lambides, and Platt 2017). These authors suggested that the potentially deleterious effects of aging on social network size was compensated for, at least among females, by their effective management navigating the social landscape thus avoiding the health-damaging effects of interpersonal conflicts. Of course, one could also argue that the declining effect of social capital on later life longevity in non-human primates reflects some of the age-as-leveller effects noted in human aging, whereby social inequalities exercise a lesser influence on later life compared with earlier adulthood and mid-life when social relations matter more (House et al. 1994; Nagel 2016).

Other studies have proposed the existence of a trade-off between reproductive activity and sociality, such that as the former declines (with age) so the latter increases. This serves as compensation, at least in the way that sociality is directed toward kin whose reproductive success might in turn be enhanced. However, as noted in the previous section, most research points to a reduction in primates’ general sociality with age. Generally, for non-human as for human societies, social capital seems to contribute to healthy aging even if the effect is less marked than that observed at earlier adult ages (Holt-Lunstad, Smith, and Layton 2010; Pradana 2022; Silk et al. 2010; Sueur et al. 2021; Thompson 2019). This effect seems to operate through several pathways, as Nicole Thompson (2019) suggests, contributing to both health and survival over the life course and across the generations as they continue into later life, even if the effects are to some degree muted by age.

Studies in human populations suggest that women retain (or acquire) more social capital than men, and generally live longer (Moon, Park, and Cho 2010; Warr 2006). In many non-human primate studies, gender differences in levels of sociality also emerge with age, such that the dominant gender retains or even increases their social capital with age, while the subordinate gender shows a steady decline (Machanda and Rosati 2020). Such gender effects may be even more marked in non-human primates, but they do not consistently favor one sex over the other as Machanda and Rosati note. One study reported a marked decline in sociality with age among females, but this arose, in large part, because sociality was present at a higher level initially in females, irrespective of age, making the decline more noticeable (Schino and Pinzaglia 2018).

Other studies of wild baboons have suggested that social affiliation has a positive effect on survival throughout adulthood and into old age (Archie et al. 2014; Silk et al. 2010). This effect applied to both same sex and opposite sex connectedness with each type of affiliation adding survival value independently (Archie et al. 2014). What is noteworthy however is the distinction between ‘social capital’ expressed as affiliation and connectedness and ‘social status’ reflected as dominance or rank. While it is found that the former shows consistent benefits to most non-human primate groups studied, and to both males and females, the impact of the latter is less clearcut with high social status having survival value for some groups but not others (Campos et al. 2020, 6). Fernando Campos and colleagues (2020) observed that while status or dominance rank had no effects on adult survival among female baboons, it had a deleterious effect on males. This suggests there is a “tradeoff” between reproductive success and life expectancy, with high-status male baboons having shorter adult lives – and hence less old age – compared with lower status males.

Age, Rank, and Status in Non-Human Primate Groups

One of the classical theories concerning patterns of change in human social aging is that of Donald Cowgill and his modernization thesis (Cowgill and Holmes 1972, Cowgill, 1974). Cowgill and Holmes suggested that the status or rank assigned to older people varied over time and across societies and was crucially dependent upon the dominant mode of production within a society at any one point in time. As societies moved from an economy based on hunting, gathering and nomadic pastoralism to settled arable farming, they suggested, the status of the older men grew as they retained ownership of farmland and farm animals, and thus ensured the transfer and succession of the family’s wealth. With industrialization and urbanization, income from wage labor, rather than wealth located in land ownership, dominated economic relations: old age lost much of its status as the earning power of younger adults outweighed considerations of land ownership. Migration to urban centers, reliance upon a wage economy and the educational and occupational skills associated with earning a living in the city favored younger adults and the status of old men declined. This thesis, however much it has been disputed, reflects a position that holds old age has no intrinsic or essential status in human societies; rather its rank or standing depends largely upon other aspects of social organization than on agedness *per se*.

Much of the literature on dominance and age in primate social groups reinforces this point – that there is no universal relationship between the two. In many non-human primate groups, in contrast to human social groups, status determination applies more to female members than to male members, because the latter often disperse to form their own troop, rarely remaining within their natal group. Among the great apes, where there is generally less dispersal, there is evidence that male dominance drops with increasing age, while females retain their position and social influence (Baker 2000, 113). Older chimpanzees and gorillas generally show less aggressive behavior irrespective of their gender or status, while some studies of Japanese monkeys have found that older high-ranking females maintain their social attraction and position with age while low ranking older females do not (Nakamichi 2003).

Some of the earliest studies of monkeys assumed that status declined with age, on account of the limited value to the troop of monkeys displaying senescent reproductive aging (Borries, Sommer, and Srivastava 1991). These authors suggested that with age, female monkeys (Hanuman langurs) lost status within their troop in terms of their limited reproductive value, only retaining status when it came to defending their troop from others. Older female monkeys “frequently sat and watched at the troop’s periphery” (Borries, Sommer, and Srivastava 1991, 252). Interestingly, they observed that the effect of reproduction in late life was somewhat to boost the status of older monkeys, in contrast to monkeys

demonstrating a quasi-menopause who fell into the lowest rank (Borries, Sommer, and Srivastava 1991, 253). This model – of declining status with increasing age – has not proved so robust, however, and other longitudinal studies have found rank more closely related to dynastic status with daughters inheriting the rank of their mothers, whatever their ages (Hausfater, Altmann, and Altmann 1982). It has been argued that dominance relations vary according to the resourcefulness of the environment, such that populations in “permissive” environments are “characterized by a degree of nepotism in female rank relations comparable to that of provisioned macaques, but in harsh environments an age-graded rank order of females” applies (Hausfater, Altmann, and Altmann 1982, 754). A more complex version of these options has been proposed, distinguishing between increasing dominance with age, decreasing dominance with age and ‘nepotistic’ hierarchies where matrilineal descent matters more than age (e.g., Broom, Koenig, and Barries 2009). Other studies have found that older female macaques are less often the recipients of aggressive behaviors but more often engaged in low-level aggression effectively deterring becoming victims of others’ attacks in a pattern of selective dominance (Almeling et al. 2017).

Like the macaques studied by Laura Almeling and her colleagues, chimpanzees display a more positive relationship, with older adult female chimpanzees exhibiting greater dominance than younger ones (e.g., Wittig and Borsch 2003). Some writers have gone so far as to describe female chimpanzee troops as a “gerontocracy” with individual adult females moving up the status hierarchy as older adult chimpanzees die off (Nishida 1989, 86). Others have questioned whether any clear or stable hierarchy can be discerned among adult female chimpanzees, and it seems unlikely that a gerontocracy model is a universal feature of chimpanzee communities. As for male chimpanzees, while several studies have observed a more stable dominance hierarchy in multi-male troops, challenges to the dominant (alpha) male occur with increasing age, and previous alpha males may accede to a drop in status whilst remaining part of the group. Indeed, some regain their status while others may simply leave the group and remain solitary, depending at least in part on the strength of their established social bonds (Uehara et al. 1994).

Studies of female gorillas have observed an inverted U-relationship, with mature/middle aged female gorillas exhibiting greater dominance ranking than either young or old adults (Robbins et al. 2005, 792). Most studies suggest that multi-male gorilla groups are rarer, as male gorillas tend to disperse leaving behind the senior male of their troop, to then form troops of their own. Hence patterns of dominance among female gorilla troops are easier to elucidate and observe over time. Male gorillas, as they age, retain their dominance because of the serial dispersal of younger males. While reports of aged males being displaced by their juniors do occur, this seems to be restricted to only a minority of cases – with the majority of alpha males dying or disappearing. The fate of elderly displaced males seems generally poor. One study reported that older displaced males “became solitary after losing their alpha status [and] subsequently died within 3 months of being usurped” (Robbins et al. 2019, 138). While such a fate is observed among other great apes, it seems clear that though age poses a greater risk from loss of status among males than females, there is no inevitability that age constitutes a decline either in activity, fitness, or indeed in dominance among the apes, nor that it constitutes a source of changing rank and resourcefulness (Thompson González et al. 2020). Equally, as Jane Goodall (1986b) observed, precious little attention or care is directed toward older frail chimpanzees by their conspecifics. If it arises, it might be said that old age plays little part in the society of the great apes.

Kinship, Social Ties, and the Grandparent Hypothesis

Bernard Thierry (1990) has argued that it is possible to identify a core dimension representing the degree of hierarchy within the social group. Some non-human primate groups exhibit strong hierarchical

status-systems, use more injurious forms of aggression in defending status positions, and show a marked preference for aggressively asserting status in non-kin interactions (effectively favoring relations with kin). Other groups, Thierry suggested, were at the other extreme, maintaining fewer and less stable patterns of dominance ranking, showing less aggression in expressing dominance, and behaving less differentially when interacting with kin and non-kin. This offers straightforward evidence that ‘nepotism’ exists in hierarchical groups, whereby intra- and inter-generational status is effectively reproduced over time (cf. Hausfater, Altman, and Altman, 1982).

In hierarchical social groups, kinship matters, and is especially evident along matrilineal relations, where cooperation rather than confrontation characterizes relations between siblings, mothers and daughters, and grandchildren and grandmothers (Kapsalis 2004; Kapsalis and Berman 1996). One of the earliest studies of grandparenting was carried out in India by Carola Borries (1988) through observations of a troop of langur monkeys which included two grandmothers who were no longer reproducing. She found that there was a conspicuous difference in the attention invested by maternal grandparents who favored female over male grandchildren. Borries suggested that grandparenting could be understood as a biologically evolved trait that favored the reproduction of the matrilineage. The ‘grandparenting hypothesis’ was first proposed by Peter Mayer (1982) in relation to the evolutionary benefits deriving from an extended period of post-reproductive life. This idea was developed further by Kristen Hawkes and her colleagues (1998), who proposed that, by extending women’s post-reproductive life, menopause enabled “senior females [to] increase the reproductive success of childbearers more than enough to offset the reduced expenditure of the childbearers themselves” (Hawkes et al. 1998, 1336). These researchers were however working with a model of menopause as a uniquely human phenomenon, of benefit to the species, rather than a more general characteristic of the primate taxa, implying that grandparenting was a specifically human, not a generic primate trait.

Although there are few clear-cut examples of discrete menopause in other primates, if applied more generally, as Mayer himself suggested, to primates demonstrating minimal or no reproduction in later life, the grandmother hypothesis can be re-framed such that “old individuals may forego the production of new offspring and instead care for their existing descendants including help for their breeding age offspring” (Peron et al. 2019, 360). In their review of mammalian grandparenting behaviors, Peron and colleagues concluded that there does seem to be evidence of some tradeoff between a longer post-reproductive lifespan and what has been termed greater “allo-nursing” or allo-parenting, that is helping care for offspring not one’s own (Peron et al. 2019, 361). Linked to this perspective of the benefits arising from preferential intra- and inter-generational relationships with kin has been speculation over the general adaptive value of grandparenting. Living long enough, it has been suggested, helps ensure that one’s adult female children have access to improved childrearing resources via grandparenting (chiefly grandmothers) and thus increases the reproductive success of the troop (Kim, Coxworth, and Hawkes 2012). Others however have argued that extended post-reproductive life is more a reflection of general longevity than it is of some special allo-parenting investment (Fedigan and Pavelka 2001). Peron and colleagues have suggested that there exists a spectrum of parental-grandparental investment, such that some species disinvest completely in reproduction and invest completely in grandparenting (humans showing the most extreme form), while others continue investing in reproduction and show no grandparenting investment (Peron et al. 2019, 365).

This evolutionary approach to grandparenting has been taken up in family studies, to form part of what has been termed ‘evolutionary family sociology’ (Rotkirch 2018). In a recent Finnish family study into human grandparent-grandchildren relationships, for example, Antti Tanskanen and Mirkka

Danielsbacka (2018) observed that differing degrees of biological relatedness were associated with both the closeness and intensity of support offered across the generations. They found that closer kin relationships predicted greater investments in grandparenting. As with much human and non-human primate research, there are many surprising parallels in social aspects of aging, despite the huge imbalance in behavioral, cognitive, cultural, and social complexity between the two species. The parallels may however lead to researchers overlooking key differences between human and non-human primates, leading in turn to a degree of unjustified anthropomorphism.

Cautions, Caveats, and Complexities

Non-human primates form and maintain social groups that take many forms, and it is no longer the case that variations in social behavior and social organization arise merely from intra-species specificity (Strier 2018a). The demography of the group, the ecological conditions they find themselves in and the particular history and lineage of the group (its mixture of incomers, leavers and hierarchical history) play a large part in how members of the group behave, how much affiliation or antagonism they show to each other, and the extent of stability experienced by their infants (Strier 2018a, 808). As research has become more attuned “to the high level of behavioral flexibility that many species exhibit” (Strier 2018b, 5), it becomes clear that non-human primate social behavior reflects a level of complexity that was scarcely grasped even a couple of decades ago.

As far as social aging is concerned, though the research base continues to be limited, there seems every reason to believe that a similar level of complexity exists between and within species of primates. As colonies and settings where basic provisions are ensured come to dominate much primatological research, it seems likely that such anthropogenic influences will introduce further unexplored sources of variability, such as the number of older animals surviving and the variety of their behavioral, physical, and social agedness. If the demographic aging of human society is becoming ever more salient in understanding contemporary society, an equivalent demographic change may well be underway, ‘in the wild’, as primate societies are increasingly managed as a series of sustainable communities (see Catherine Hill [2002] for a useful debate about the ethics of sustainable communities). Given the consistent evidence that mammals raised in captivity live considerably longer than do their conspecifics in the wild, that reproductive senescence occurs earlier and more completely in the wild than in captivity, and that dominance hierarchies adopted to ensure reliable food supplies and safety from predators are much less necessary in sustained communities, it is not improbable that primates’ social behavior and organization will continue to change, and this will most likely include changes in forms of social aging (Atsalis and Videan 2009).

Social scientists were once fiercely critical towards the sociobiology promoted during the 1960s and 1970s (Caplan 1976; Gove 1987). Consider how the situation has changed in the twenty first century, with the increasing human influence on non-human primate society: on the one hand the destruction of the natural habitat and on the other the increase in protected and provisioned areas suggests that it no longer makes sense to presage an understanding of human society upon its precursors. Rather, it seems necessary to consider the endless entanglement of nature and society as a persistent and pervasive feature of primate life, with an accompanying inter- and intra-species diversity and diffusion taking place in the context of the shrinking habitat that previously sustained non-human primate societies. A future ‘unwinding’ seems probable, as life outside conserved areas becomes, for most non-human primates, increasingly precarious (Carvalho et al. 2021; IUCN 2020; Junker et al. 2020). The global dominance of one species (*homo sapiens*) over all other species of primate seems likely to fulfil Alison Jolly’s prediction that “we will more and more be studying non-human primates as affected by human primates...[as] looking at primate social behavior in the face of human-induced change will

soon be respectable” (Jolly, as cited in Pollock 2015, 213). This will no doubt include the study of human interventions that modify patterns of demographic and social aging in non-human primate society in ways that may be surprisingly difficult to predict, let alone adjudicate (Nelson 2017). Aging, both social and biological, is changing more rapidly now than at any previous time; that is perhaps the most important common denominator for all human and non-human primates.

Conclusions

The aim of this paper has been to consider whether and how far the study of social aging in non-human mammals (mainly other primate species) might aid understanding social aging in human societies. While animal models are widely used to study the biological processes of aging and their relevance to human aging, aging in non-human social groups has rarely been used to illuminate human social aging. This paper suggests that, based on its literature review of studies of social aging in non-human primate societies, at least four themes can be identified which have potential relevance for aging studies, social gerontology, and the anthropology of old age. These are (a) evidence of social disengagement with age; (b) the returns of social capital in aging well; (c) the relationship between age and rank or status within the social group’ and (d) the role of post-reproductive ‘grandparenting’ in enhancing health and survival across the generations.

Given that primates constitute some of the longest living mammalian species on earth, and hence are most likely to reach and live through a period akin to old age, it seems plausible to consider this sort of evidence for illuminating old age as a conserved status within social groups in human as well as non-human primate society. Critical to such consideration is the conceptual status of aging and old age in non-human primates’ social groups. Do primates other than humans recognize agedness as a salient characteristic of their conspecifics and if so, is there evidence that such recognition alters their behavior? The evidence for the recognition of old age – as distinct from adulthood or maturity – in non-human primates is in fact not very strong. Yet, as Mary Pavelka noted some decades ago, “there is little evidence that the behavior of the aged [monkey] females differs significantly from that of other adult females, and it does not appear that the fact of biological aging creates any radically different social situation” (Pavelka 1990, 363). It is remarkable how rarely, at least until recently, non-human primates’ agedness or old age has even been commented upon, let alone enabled a stage of life termed ‘old age’ to be defined or described by primatologists on grounds other than known chronology or post-mortem examination. This problem of recognition poses a major challenge in studies of social aging in non-human primates and constrains the relevance of such studies to contemporary aging studies, social gerontology, and the anthropology of later life. Concepts such as age discrimination and ageism seem to have little relevance outside of human societies, suggesting there is no inherent dislike, disregard, or hostility toward the aged in non-human societies.

At the same time, there are numerous examples of human-like processes – from age-associated change in social status to the value of sociality on primate longevity, and from evidence of grandparenting to signs of social disengagement. Most importantly there is growing evidence that patterns of social aging in both non-human and human social groups are more open and flexible than has perhaps been acknowledged, including the often quite marked impact that human behavior and culture can have in shaping non-human primate aging. While the grandparenting hypothesis implies a degree of evolutionary reductionism that should certainly be treated cautiously, the complex interplay between age, gender lineage, and ecological resources illustrates just how variable the links are between rank or status, social relations, and older age. Differential effects on social behavior between juvenile, mature, and older primates repudiate any simple evolutionary reductionism. However, this also suggests that independent of social cognition (or collective representations), behavioral change may arise, in part at

least, from the ecology of the group, its gendered constitution, the extent of post-reproductive senescence alongside more general patterns of affiliation, and antagonism evident within the group. Human interpretations of age rank and status have long been written about, including the notion that once upon a time and/or in some other society, those deemed ‘aged’ were treated with great respect, usually by older men lamenting their loss of power. Such collective and uniquely human representations (or social imaginaries) may in fact be post-hoc explanations for patterns of behavior shared by us all.

While it has become abundantly clear that there is indeed aging in the wild, what has also become clear is that ‘the wild’ is itself a more complex entity, reflecting a mixture of ecological factors – the scarcity or plenitude of resources, the degree of predation and level of intra-species competition as well as inter-species variability in the rate of living and of aging – alongside increasing human impact on that ecology. As non-human primates living outside protected areas face increasing risks of extinction, in large part because of human behavior, so the demographic and behavioral aspects of non-human primate aging are likely to change, perhaps, and somewhat paradoxically, contributing to the aging both of human and non-human primate societies. Bearing this duality in mind, it is possible that a comparative social gerontology of human and non-human primates can be envisioned, not so much by basing models of human aging on the non-human world but by recognizing that both monkeys and apes (including ourselves) “are indeed unified by behavioral and demographic social flexibility” (Malone, Fuentes, and White 2012, 1253). There is a growing two-way interchange between the human and non-human world that is based less on mechanisms of evolutionary selection than on a shared heritage of social complexity and flexibility, a point that is as applicable to the ordering and organization of the life course as it is to the social world more generally (Bronikowski et al. 2011). How far old age in non-human primate societies can be seen as the internal product of those societies and how far both it and the ‘aging societies’ in which old age appears are being realised principally as the co-products of human society remains to be seen. This is of course speculation but the more the wild becomes a series of conserved and protected spaces engineered and ensured by human agency, the more one wonders whether or not all primate old age may be becoming a kind of human old age, after all.

Notes

1. Among primates, a broad division can be made between apes (bonobos, chimpanzees, gibbons, gorillas, humans, and orangutans) and monkeys (baboons, capuchins, colobus, macaques and marmosets. The apes have a later onset of fertility (10-30 years) greater longevity (50 years +) and a longer period of senescence (35-50 years) than monkeys (5-20 years, 25 years + and 20-35 years respectively) as outlined in Washburn (1982, 13). For further classificatory details see the Appendix.

2. The empirical literature reviewed here draws upon the major primatology and physical anthropology journals – *The American Journal of Primatology*, *The American Journal of Physical Anthropology*, *Folia Primatologica*, *The International Journal of Primatology*, *Neotropical Primates and Primates* – from 1990 to 2022. The intention was to cover relevant empirical research on primate societies, but not to conduct a systematic review of all the empirical research in this emerging field. Rather the aim was to derive the main themes relating to social aging – and link these to themes in social gerontology. The overall goal was to critically examine how closely aging in non-human primate society can be aligned with, or distinguished from, aging in human society.

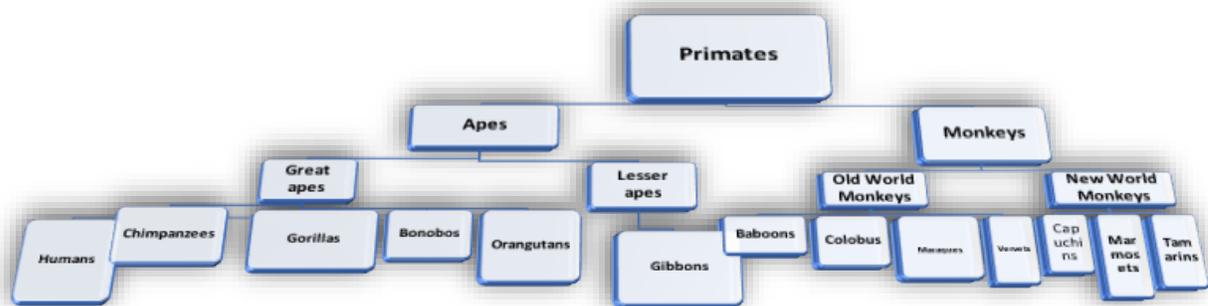
3. Draws distinguished between *dominance* as “an attribute of the pattern of repeated, agonistic interactions between two individuals, characterized by a consistent outcome in favour of the same dyad

member and a default yielding response of its opponent” and *dominance as rank* (or status) namely, “the position of one individual in a dominance hierarchy” (Drews 1993, 308).

Appendix

Taxonomy of Major Primate Groups

The major division of the order of primates is between the family of apes and that of monkeys (the latter are smaller, have tails and live a largely tree bound existence). Both old and new world monkeys have smaller bodies, brains and shorter lifespans compared with apes. Among the lesser apes, the only major species are the gibbons. Among the family of great apes, orangutans are considered a distinct sub-family, while chimpanzees, gorillas and humans together form the main species making up the sub-family of *Homininae* (Groves 2018).



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