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Long-sightedness in old wild bonobos during grooming

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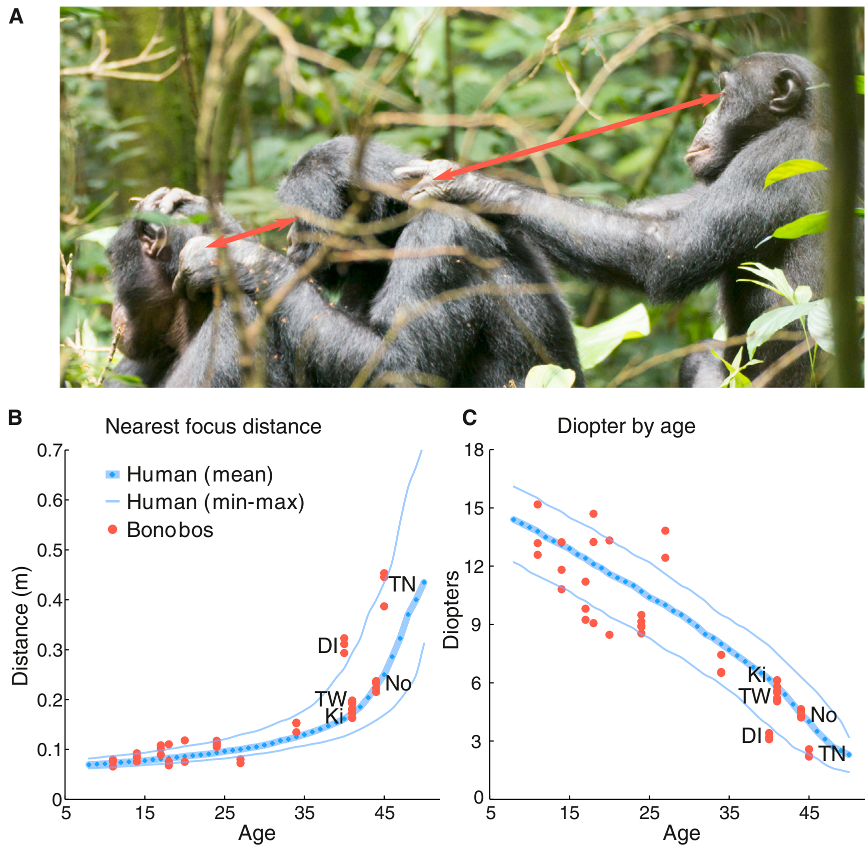

Figure 1. Grooming distance of bonobos and comparison with humans
(A) Grooming distance (red arrows) is defined as the distance from an individual's eyes to their fingers. The difference in grooming distance of TN (45 years old; right) and GC (27 years old; middle) is easily noticeable. A video clip of this grooming event is available at the following link (https://youtu.be/Mw6bYOeML3g). (B) Grooming distance of bonobos (red dots) increases with age. It is very similar to the nearest focus distance calculated from diopters (1m/diopters) in humans (blue dots and lines). (C) Amplitude of accommodation (diopter) of bonobos (red dots), calculated by (1m/grooming distance in meters) is very similar to humans (blue dots and lines). The human data are from Duane's work which excluded extreme values to calculate minimum and maximum values [7]. A human diopter is the reciprocal of the nearest focus distance (1m/focus distance in meters) and that of the bonobo is reciprocal of the grooming distance. Please see the Supplemental Information for more details.

Some scientists have suggested that, among Hominidae, prolonged postmenopausal longevity evolved uniquely in humans [1], while others disagree [2]. There have, however, been few empirical studies on how physiological aging and somatic durability in humans compare to our closest relatives — chimpanzees and bonobos [3]. If prolonged lifespan is selected for in humans, physiological aging, including reproductive and somatic senescence, might be different for *Pan* and *Homo*. But it seems that the parameters of reproductive senescence, such as the age of having their final offspring and the number of years between generations, are not very different between chimpanzee and human females [4]. Here, we report evidence for five cases of long-sightedness (presbyopia) in old wild bonobos, exhibited during grooming. Our results suggest that senescence of the eye has not changed much since the divergence of *Pan* and *Homo* from their common ancestor.

Presbyopia is defined as a decline in the refractive power of the crystalline lens with age, which decreases one's ability to focus on near visual tasks. Anecdotal evidence of presbyopia in old female chimpanzees is available from two wild populations: Jr, a 50-year-old in Bossou [5]; and CA, a 52-year-old, and WX, a 44-year-old, in Mahale [6]). These reports did not, however, provide quantitative measurement and systematic comparison of the distance between the groomer's eyes and fingers (referred to as 'grooming distance' hereafter; Figure 1A), nor did they track the onset and progression of presbyopia. Furthermore, comparative studies on senescence of the eyes in our closest relative could provide insights into understanding the evolution of human senescence.

To address these methodological concerns, and highlight the importance of comparative studies, we first quantitatively measured, using digital photography, the grooming distance of 14 wild bonobos from 11 to 45 years of age. Second, we analyzed how grooming distance varied in relation to age and sex in bonobos and compared it with nearest focus distance in humans. We photographed each individual's ear and then photographed a ruler at the same distance that the individual had been sitting (see Supplemental Information). We then took photographs of individuals while grooming, and used their own ear length measurements to calculate the grooming distance.

We found that grooming distance exponentially increased with age, and amplitude of accommodation (diopters) decreased linearly with age (Figure 1B,C; Table S1). We did not find any effect of sex. This is consistent with the finding from humans that there is no sex difference in the progress of presbyopia despite the sex difference in longevity [7], though we may not have enough data to conclusively rule out such differences. As an aside to our study, we noted that the ear length of bonobos did not vary in relation to age (Table S1), which is different from humans whose ears tend to get larger as they get older [8], although this may be because the human data included individuals over 60 years old. The five old bonobos (over 40 years old) had significantly greater grooming distances than younger individuals (Table S1; see also grooming videos of all subjects at http://goo.gl/IX0O87). Grooming distance could therefore serve as a useful tool for distinguishing old individuals in newly established bonobo (and probably chimpanzee) study sites.

In this study, we were missing longitudinal data of individuals throughout their lifetimes, but we did have a video clip taken in 2009 of 35-year-old Ki grooming. We took four snap shots from the video and measured grooming distance. As we did not measure Ki's ear length in 2009, we assumed that her ear length in 2009 was the same as in 2015, which is plausible given that we found no difference of ear length with age. We found that Ki's grooming distance in 2009 (11.91 ± 0.83cm) was significantly shorter (Wilcoxon signed-rank test; $W = 0$, $p = 0.029$) than that of Ki in 2015 (16.95 ± 0.78cm). This is compelling evidence that Ki's grooming distance had indeed increased with age, and it also suggests that bonobos probably groom at the nearest focus distance (Supplemental Experimental Procedures), and visual inspection during grooming is essential, although tactile sensation may also play an important role.

Together with the result from the exponential model, our findings imply that grooming distance increases rapidly from late 30s to early 40s in wild bonobos, suggesting that presbyopia is not a by-product of the modern human lifestyle, which demands near visual tasks. This pattern found in bonobos is strikingly similar to that of humans (Figure 1B,C) from Duane's pioneering work on the human eye in 1922 [7]. We therefore conclude that the development and progression of presbyopia in wild bonobos is similar to presbyopia in humans.

Male chimpanzees in the wild do not usually reach their 40s; however, in our study three male bonobos were over 40 and had developed presbyopia. It is possible that peaceful bonobo society, characterized as cohesive and tolerant compared to that of chimpanzees [9], might ease the life of the elderly and allow male bonobos to live longer. Long-term field studies and collaboration across field sites would allow us to determine whether longevity is indeed different between bonobo and chimpanzee males. This may be one of the key questions to understanding the prolonged postmenopausal lifespan of *Homo*, as longevity may be influenced by social characteristics, in that cohesive and mild social environments may allow individuals to survive longer.

Comparison of accommodation amplitude between rhesus macaques and humans reveals a similar aging pattern, but only when scaled for lifespan and diopters [10]. However, we found no need to correct for lifespan and diopters when comparing between bonobos and humans; senescence of the eyes in wild bonobos closely resembles the pattern of modern humans. Alongside these findings, our report highlights the necessity of further comparative research into other aspects of somatic and reproductive senescence for more Hominidae species in the wild and captivity, with a particular focus on the importance of mild and tolerant socio-ecological environments for the elderly. Further comparative research will allow us to understand how the prolonged postmenopausal lifespan of modern humans, and differences in refraction of the eye across primate species, have been shaped by evolution.

SUPPLEMENTAL INFORMATION

Supplemental Information includes one figure, one table and experimental procedures and can be found with this article online at http://dx.doi.org/10.1016/j.cub.2016.09.019.

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