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Old age variably impacts chimpanzee engagement and efficiency in stone tool use

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eLife Assessment

This **valuable** study provides a novel framework for leveraging longitudinal field observations to examine the effects of aging on stone tool use behaviour in wild chimpanzees. The methods and results are robust providing **solid** evidence of the effects of old age on nut cracking behaviour at this field site. Despite the low sample size of five individuals, this study is of broad interest to ethologists, primatologists, archaeologists, and psychologists.

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Abstract

We know vanishingly little about how long-lived apes experience senescence in the wild, particularly with respect to their foraging behaviors, which are essential for survival. Some wild apes use tools during foraging and, given the additional cognitive and physical challenges presented by tool use, we predict that such behaviors are at a heightened risk of senescence. However, until the present, longitudinal analysis of the effects of progressive aging on wild ape tool-use behaviors has not been possible due to a lack of available data. In response to this research gap, we sampled data from a longitudinal video archive that contained footage of wild chimpanzees engaging in one of their most complex forms of tool use - the cracking of hard-shelled nuts with hammers and anvil stones, termed *nut cracking* - at an 'outdoor laboratory' at Bossou, Guinea. By sampling data over a 17-year period, we

describe how the extent to which wild chimpanzees engage in – and efficiently perform – nut cracking changes between the ages of approximately 39-44 to 56-61 years of age. Over this extended sampling period, chimpanzees began attending experimental nut cracking sites less frequently than younger individuals. Several elderly chimpanzees exhibited reductions in efficiency across multiple components of nut cracking, including taking more time to select stone tools prior to use, and taking longer to crack open nuts and consume the associated pieces of kernel. Two chimpanzees also began using less streamlined behavioral sequences to crack nuts, including a greater number of actions (such as more numerous strikes of the hammer stone). Most notably, we report interindividual variability in the extent to which elderly chimpanzees' tool-use behaviors changed during our sample period – ranging from small to profound reductions in tool engagement and efficiency – as well as differences in the specific aspects of nut cracking behaviors that changed for each individual as they aged. We discuss the possible causes of these changes with reference to research into senescence in captive primates, and provide future directions for research of primate aging in both captive and wild settings.

1. Introduction

Senescence can be understood as a reduction in the efficacy of biological systems with increasing age. In recent decades, the senescence of non-human primates (henceforth primates) have been a point of considerable research interest[1–3]. In part, this is due to the fact that primates offer uniquely translatable models for understanding the nature and evolution of human senescence, given their high genetic, physiological, and behavioral similarities[1,4–6]. Accordingly, many parallels between the senescent processes of humans and primates have been uncovered, including in their cognition[7–12] physiology[1,13–15], and their resultant behaviours[16–20]. However, thus far, the majority of these studies have focused on captive populations of short-living species, and exploit existing variation in age among individuals to infer the effects of senescence through cross-sectional analyses[1,8,21,22]. Comparatively few studies have investigated how senescence influences behaviors of primates in the wild (with the exception of a handful of examples[23–27]), and even fewer employ longitudinal data sampling to understand how senescence leads to changes in the behaviors of specific individuals over time. These studies of wild individuals are highly valuable as they shed light on how aging affects the day-to-day behaviors that primates rely on for survival – conclusions which cannot be easily predicted from studies from captivity, given that patterns of physiological senescence can differ significantly between captive and naturalistic environments[28,29]. Further research is therefore required to understand how aging influences the lives of wild primates. This is particularly true for long-living great ape species, which are underrepresented in the existing literature, yet their phylogenetic proximity to humans means that they likely offer the most suitable models for understanding the evolution of the human aging process.

Of the day-to-day behaviors of great apes, the combined physical and cognitive demands of tool use make it likely to exhibit particular changes with progressive old age. The tool-use behaviors of great apes are highly challenging, requiring tool users to draw upon a wide array of high-level cognitive abilities, including planning and the flexible assembly of actions into goal-directed behaviors[30–33]; an understanding of causal relationships between objects[34–36]; as well as knowledge of the physical properties of objects and how to exploit these properties to use tools successfully[32,37–39]. Many of these cognitive abilities – including the more specific subcomponents of these abilities, such as motor coordination[12], working memory[40], executive functioning[10], and cognitive flexibility[11] – have been identified as at risk of senescence in captive living primates; however, never in tool-use behaviors themselves. Moreover, physiological changes including reduced bone mass[13,15,41], muscle wasting (sarcopenia[15,42,43]), the development of arthritis[15], and reduced visual acuity[23] have been identified in a number of primate species, including great apes, which all influence individual strength, dexterity, and

accuracy of movement. These findings suggest that tool use could be a domain of great-ape behavior that is at specific risk of senescence; however, it has not yet been possible to address this question due to an absence of long-term data on great ape tool-use behaviors that also include instances of tool use performed by elderly individuals.

To address this gap in the literature, we used a longitudinal archive of video footage of wild, West African chimpanzees (*Pan troglodytes verus*) using stone tools to crack hard-shelled nuts as part of a decades-long field experiment in a clearing in the Bossou forest, Guinea[44,45] ('the outdoor laboratory'; see Methods section 4.1 and **Fig. 1** for information about the experimental set up at the outdoor laboratory). Nut cracking is one of the most sophisticated forms of tool use observed in the animal kingdom, and is habitually performed by a number of primate species in the wild including several communities of chimpanzees[37,46,47] (*Pan troglodytes*), capuchin monkeys[48–52] (*Cebus* and *Sapajus* spp.), and long-tailed macaques[53,54] (*Macaca fascicularis*). During nut cracking, a nut is placed on a hard substrate (for the chimpanzee population used in this study, this substrate is a portable anvil stone, though at other sites this may be a root or rocky outcrop[37,39]), before being struck repeatedly with a hammer stone until the nut is cracked open and the edible kernel inside extracted and consumed (see **Fig. 1a**). Nut cracking is learnt by chimpanzees at Bossou by the age of seven years (often between 3.5 and 5 years of age[55,56]), and chimpanzees continue to perform this behavior throughout their lives[44]. This life-long engagement in nut cracking permits characterization of how individual chimpanzees perform this behavior across their lives[57], including during the oldest years of their lifespan. Nut cracking features all of the key elements of tool-use behaviors which we predict will make them likely to senesce with old age, including the need to construct complex object associations[34,35,58]; to organize and address multiple goals using an extended behavioral sequence[32,33]; to select tool objects based on perceived properties[32,37,39], and to combine objects with sufficient dexterity, precision and force and to crack nuts without knocking nuts off the anvil, or smashing interior kernels[38].

To determine whether – and if so, how – old age influenced the nut cracking behaviors of wild chimpanzees, we sampled video footage collected at the outdoor laboratory in five field seasons spanning a 17-year timeframe between 1999 and 2016. During this timeframe, we collected longitudinal data on five chimpanzees as they aged from approximately 39-44 years old (end of mid-life) to 56-61 years old (ages which are close to the maximum for wild chimpanzee lifespans[59]). Across sampled field seasons, we estimated how readily chimpanzees engaged in nut cracking behaviors using two key metrics: the frequency which chimpanzees visited outdoor laboratory sites during each field season (compared to a control group of younger individuals between the ages of 8 and 30 years of age), and when present, the proportion of time chimpanzees spent engaging with nuts and stone tools compared to other key behaviors (such as drinking water from an available water point using leaf tools[60] and eating oil-palm fruits that are provisioned alongside nuts; see **Figs 1b** & 1c). We also measured how quickly chimpanzees selected stone tools from a central matrix of over 50 stones (a generalized metric of efficiency during tool selection; see **Figs 1d** & 1e), as well as how efficiently chimpanzees cracked open nuts using stone tools and consumed the associated kernel.

Overall, with increasingly old age (measured by progressive field seasons), elderly chimpanzees were significantly less likely to visit experimental nut cracking sites. In comparison, younger individuals (i.e. younger adults, and older immatures who had learnt how to crack nuts) exhibited no change over successive field seasons, suggesting that this reduced attendance at experimental nut cracking sites was confined to an elderly, aging cohort of chimpanzees. When present at the outdoor laboratory, two of our five elderly individuals spent substantially less time engaging in nut cracking at older ages, as compared to their behaviors in previous field seasons. Moreover, several elderly chimpanzees took more time to select stone tools in later field seasons than in earlier field seasons, and were also less efficient at using stone tools to crack open oil-palm nuts. Importantly, we detected considerable interindividual variability in the effects of aging on how

Figure 1.

The experimental set-up and behaviors at the outdoor laboratory.

(a) Yo, an elderly female (approx. 51 years old), has placed a coula nut (*Coula edulis*) on an anvil stone, and is preparing to strike with the hammer stone. (b) An adult female (14 years old) using a leaf tool to drink water from the water point. (c) Yo and Velu (left to right, both approximately 56-58 years old), eating oil-palm fruits from an available raceme. (d) The central stone-tool matrix with numbered stones. (e) Yo (right; approximately 49 years old) selecting tools from the stone matrix.

readily elderly chimpanzees engaged with nuts and stone tools, how quickly they selected tools, and the efficiency with which elderly chimpanzees used tools. Some individuals demonstrated little-to-no change in engagement and efficiency with aging, whereas others experienced significant changes across different aspects of their nut cracking behavior. We discuss our findings in the context of existing literature for primate aging, and hypothesize which factors underpin observed changes in behavior, including cognitive, physiological, and motivational causes, and generate a number of suggested avenues for further study. We also discuss how aging can likely compound existing interindividual differences in the proficiency of socially-learnt technical skills in non-human animals, and discuss how tool use could present a suitable indicator for identifying individuals who are experiencing the effects of profound senescence in the wild.

2. Results

2.1 Sampled data

We sampled five timepoints separated by intervals of 3-5 years (field seasons 1999-2000, 2004-2005, 2008-2009, 2011-2012, and 2016-2017; with each field season referred to hereafter by its initial year). The exact age at which chimpanzees may be considered 'old' is a point of continued debate. However, chimpanzees are generally considered to begin entering old age at approximately 40 years old[43,61,62], after which survivorship begins to decrease more rapidly than earlier in adulthood[59]. We therefore confined our analysis to individuals who were above at least 30 years of age in at least three of the five sampled field seasons. This sample allowed us to collect data longitudinally, beginning with ages where chimpanzees are in the prime of adulthood, and spanning into old age. Under these criteria, we were able to include four old-age females (Fana, Jire, Velu and Yo) and one old-age male (Tua) in our analyses. All five of these individuals were present at Bossou when the long-term research project was established in 1976; as a consequence, their birth years are estimates based on physical growth characteristics at the time of first observation (see **Table 1**). Given that these estimated birth years range from 1956 to 1961, these individuals are estimated to be between 39-44 years old at the start of our sampling window (1999), and therefore are entering the window of 'old age'. By 2016, estimated ages ranged from 56-61 years old, reflecting an age which is near the maximum for wild chimpanzees. All four females were present at Bossou throughout the entire sampled time-frame for our analysis; however, Tua, the only adult male, disappeared in September 2013 (presumed dead). Therefore, data for Tua spans a shorter time frame between the 1999 and 2011 field seasons. As all five focal individuals' ages are within five years of each other (and therefore similar estimates), we use the progression through field seasons as a proxy for increasing age, and treat all individuals as similarly 'old' at each field season.

A summary of sampling effort for each chimpanzee in each field season can be found in **Table 1**, including their estimated ages in each field season (and subsequent year of death), the number of encounters sampled for behavior coding for each individual (between 10 and 1 per individual per field season; median = 10), the total duration each individual was observed during the field season (mean = 280.6 minutes per individual per field season; SD = 83.3 minutes), and the number of nuts that they were observed cracking (between 141 and 5 nuts per year; median across individuals and field seasons = 80).

2.2 Attendance at the outdoor laboratory

We modelled the rate at which focal old-aged chimpanzees attended the outdoor laboratory over progressive field seasons, whilst controlling for the total length of each field season. We compared this relationship with attendance data from younger individuals (between the ages of 8 and 30 years; see **Fig. 2a**). This younger cohort acted as a baseline control for changes in attendance rate at the population level that are unlikely to be due to senescence. In each sampled field season,

ID	DOB*	Date of Death (Age)	Age (years)					Observed Encounters (% including interaction with nuts or stone tools)					Total Time Observed (minutes)					Action Sequences Coded (for individual nuts)				
			1999	2004	2008	2011	2016	1999	2004	2008	2011	2016	1999	2004	2008	2011	2016	1999	2004	2008	2011	2016
Fana	1956	2022 (67)	44	49	53	56	61	10 (70%)	10 (70%)	10 (80%)	7 (28.6%)	10 (40%)	280.6	275.2	184.2	105.7	283.5	80	77	80	-	70
Jire	1958	Alive as of 2025 (67)	42	47	51	54	59	10 (80%)	10 (80%)	10 (90%)	10 (60%)	10 (80%)	339.4	349.9	275.0	282.1	308.6	100	91	104	42	82
TUA	1957	2013 (56)	43	48	52	55	-	10 (70%)	10 (80%)	10 (80%)	5 (60%)	-	174.4	212.1	204.3	116.0	-	103	96	81	26	-
Velu	1959	2017 (58)	41	46	50	53	58	10 (60%)	10 (80%)	7 (85.7%)	1 (100%)	7 (42.9%)	189.4	281.8	158	23.1	202.4	85	99	50	-	5
Yo	1961	2021 (60)	39	44	48	51	56	10 (80%)	10 (70%)	10 (90%)	3 (33%)	5 (40%)	200.7	304.5	363.7	211.3	282.7	66	70	141	20	33

*Date of birth (DOB) was estimated for these individuals at the start of longitudinal data collection at Bossou (1976). Thus, ages for individuals are estimates. Ages are approximated from January of the estimated year of birth, and the end of the final month of each field season (e.g. for the 1999-2000 field season – abbreviated to 1999 - ages are estimated using 29th February 2000 as the end of the field season).

Table 1.

Summary of sampled observations for each focal old-age individual.

Total time observed includes all time individuals were present in the first 10 encounters of each field season (Observed Encounters). Dashed lines (-) represent where no data was collected for an individual in a given field season. Males have names in all capitals, whereas females have names in capitals and lower case.

Individual	Sex	Attendance	Engagement	Tool Selection Time	Oil-Palm Nut Cracking			Summary
					Total Time	# Actions	# Strikes	
Fana	F	Decrease	Decrease	Increase	Possible mild increase	-	-	Rate of attendance at the outdoor laboratory decreased, and Fana engaged with nuts and stones less often when present. Fana took longer to select tools. However, her general tool-using efficiency was mostly constant.
Jire	F	Decrease	Possible Mild Decrease	Increase	Mild increase	-	-	Rate of attendance at the outdoor laboratory decreased. Jire took longer to select stone tools. General tool-using efficiency was mostly constant, but Jire took slightly longer to crack oil-palm nuts in later years.
TUA	M	-	Possible Mild Increase	Decrease	-	-	-	Tua became slightly faster at selecting tools, and his tool-using efficiency was constant across years.
Velu	F	Decrease	Decrease (although sample size was small in 2011)	-	Increase	Increase	Increase	Rate of attendance at the outdoor laboratory decreased. Velu engaged with nuts and stones less often when present. Velu took longer to crack oil-palm nuts, and used more striking actions.
Yo	F	Decrease	Possible Mild Increase	Increase	Increase	Increase	Increase	Rate of attendance at the outdoor laboratory decreased. When present, Yo spent a slightly greater proportion of time engaging with nuts and stones. Yo took much longer to select tools, and demonstrated the largest reduction in tool-using efficiency.

Table 2.

Summary of changes observed in each chimpanzee with progressive aging.

Summaries describe the differences between the first and last field season each individual was sampled (although models underlying each result used data from all field seasons). The term 'Possible Mild Increase/Decrease' is used to note where we identified a change for a particular metric, but this change was considerably smaller than for other individuals, and therefore could be due to chance. We address these instances on a case-by-case basis within the Results. Names of males are listed in all capitals; females' names are in capitals and lower case.

the number of individuals over the age of 30 (older cohort) varied between five and six individuals, whereas the number of chimpanzees between the ages of 8 and 30 years (younger cohort) varied between five and two individuals.

In 1999, chimpanzees in the older cohort had a marginally lower attendance rate than younger cohort (encounters/day: older cohort = 0.68; younger cohort = 0.74). However, by 2016, this difference was much larger, with older chimpanzees being less likely to visit the outdoor laboratory compared to younger individuals (encounters/day in 2016: older cohort = 0.32; younger cohort = 0.53; see **Fig. 2b** for data from each elderly individual). Correspondingly, a model of attendance rate over successive field seasons (including data across all field seasons) identified a significantly greater decline in attendance rate for the older cohort across successive field seasons as compared to the younger cohort (interaction effect of field season and age-cohort: $z = -2.285$; $p = 0.022$; see Table S2 for full model output). Conversely, we found no evidence of a decline in attendance rate for chimpanzees in our younger cohort over successive field seasons ($z = -1.572$; $p = 0.11$). We confirmed the importance of this interaction effect by comparing the fit of the full model with a model lacking the interaction effect between age-cohort and field season (therefore assuming an identical relationship across field seasons for both cohorts) and a null model (which assumed no effect of field season). AIC comparison confirmed that the model which included an interaction effect offered the best explanation of the data relative to model complexity ($AIC_{Interaction} = 340$; $AIC_{Interaction\text{-}removed} = 343$; $AIC_{Null} = 376$). All four elderly female chimpanzees exhibited attendance rates that were lower in 2016 than in 1999; however, for Tua (the elderly adult male), attendance rates in his earliest and latest field seasons were approximately equal (1999 = 0.48 encounters/day; 2011 = 0.5 encounters/day; see **Fig. 2b**).

2.3. Behaviors at the outdoor laboratory

We measured how the proportion of time each elderly individual spent interacting with nuts and stones when present at the outdoor laboratory changed over successive field seasons (see **Fig. 2c**). By 2011, the final year of this analysis (we omitted the use of 2016 for this analysis, see methods), two old-aged individuals (Fana and Velu) spent substantially less time engaging with nuts and stone tools (% time engaging with nuts and stone tools in each season; Fana: 1999 = 62.3%; 2011 = 15.6%; Velu: 1999 = 51.6%; 2011 = 5.0%). We did not observe either individual successfully cracking any nuts at the outdoor laboratory in 2011. Most interactions with nuts and stone tools involved scavenging kernels from the ground (produced by other individuals' nut cracking behaviors), or in the case of Velu, a short attempt to crack open a nut, before ceasing the behavior and feeding from oil-palm fruits. Correspondingly, in 2011, Fana spent more time engaging in 'Other' behaviors, such as resting and grooming (+38.3% of total time in 2011 compared with 1999), whereas Velu spent more time eating palm fruits (+35.5%) and drinking water from the water point (+25.8%; note that data for Velu come from a single encounter in 2011, so proportions should be interpreted with caution). Conversely, three individuals spent similar proportions of time engaging with nuts and stone tools when present at the outdoor laboratory (change in % time between 1999 and 2011: Jire = −5.5%; Tua = +6.9%; Yo = +8.9%). For these individuals, the small-scale changes in total time engaging with nuts and stones are more likely to be the product of chance fluctuation in engagement across field seasons.

2.4 Tool-selection time

Chimpanzees select stone tools based on their physical characteristics such as raw material, size, and weight[32,37,39,63]. Therefore, stone-tool selection at the central stone matrix represents a complex decision-making task where chimpanzees must evaluate an extensive set of options (over 50 total stones). Between 1999 and 2016, we recorded the duration of 108 stone-tool selection events across 49 encounters for the five focal old-aged individuals (see **Fig. 3a**, and Table S3). A mixed-effect model with the year of the field season as both a random intercept and random slope for each individual offered the best explanation for the total variation in the time taken to select tools (see **Fig. 3b** for a visualization of the random slope model). This model

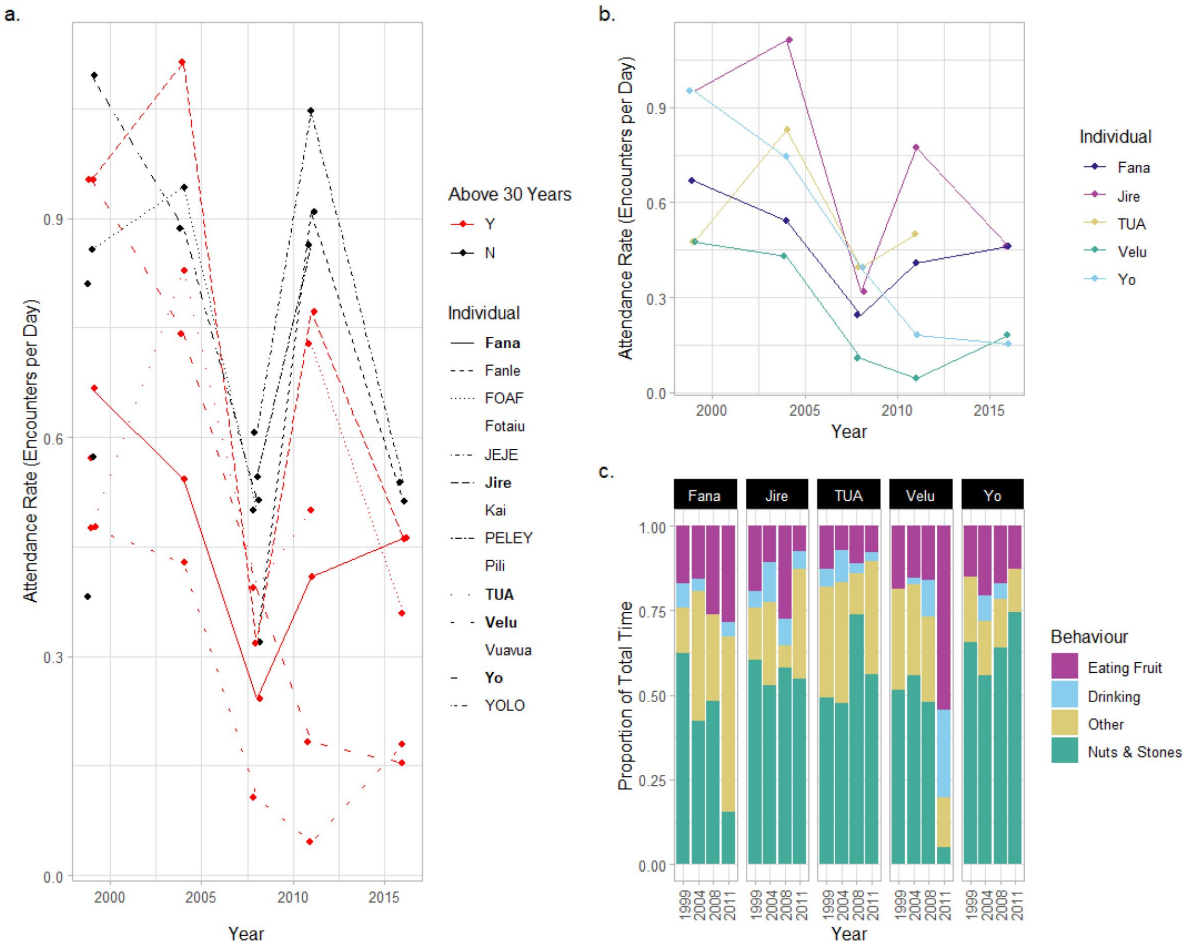

Figure 2.

Attendance and behavior of old-aged chimpanzees at the outdoor laboratory.

(a) Attendance rate for individuals at the outdoor laboratory between the 1999 and 2016 field seasons. Red points and lines indicate individuals are over 30 years old; black points and lines indicate individuals younger than 30 years. Lines are drawn for all individuals who attended the outdoor laboratory in two or more field seasons (individuals who were only sampled in one field season have blank spaces in the legend). The names of males are provided in all capitals, and females are provided with capital and lower-case letters. Focal old-aged individuals are indicated in the legend in bold. **(b)** Attendance data for the five focal individuals as they age from 1999 to 2016. **(c)** The proportion of total time individuals spent engaging in four different categories of behavior at the outdoor laboratory between 1999 and 2011 (data collected at the first outdoor laboratory location only).

outperformed a null model which assumed no effect of field season ($AIC_{Year\text{-}RandomSlope}$ = 231; AIC_{Null} = 234) as well as a model which included a fixed slope for field seasons – and therefore the same aging effect - across all individuals (where models were refit by restricted maximum likelihood to improve the accuracy of random-effect estimation; $AIC_{Year\text{-}Random}$ = 244; $AIC_{Year\text{-}Fixed}$ = 246; see Tables S4-S6 for model summaries). The best explanation for our data is therefore one where aging has a significant effect on tool-selection time; however, the effects of aging differ between individuals. The random-slope model identified that Yo underwent the greatest increase in stone-tool selection time across sampled field seasons, followed by Fana and then Jire. Velu exhibited relative consistency in the duration of stone-tool selection across field seasons, and the only individual to show a negative relationship between the duration of stone-tool selection and increasing years was Tua.

2.5 Efficiency processing oil-palm nuts

Across the five focal elderly chimpanzees, we recorded sequences of actions used to crack 1601 individual nuts (1538 oil-palm nuts and 63 coula nuts). As coula nuts were only provided alongside oil-palm nuts in one sampled field season (2011), we filtered data to include only the 1538 oil-palm nuts when modelling the influence of progressive old age on the efficiency of nut cracking, and describe data on the cracking of coula nuts separately (see supplementary materials).

For three efficiency metrics, models that contained the year of the field season as a fixed effect outperformed null models which assumed no change across years (models were fit using data from all field seasons). These metrics included the total time taken to crack and process nuts (AIC_{Year} = 3086, AIC_{Null} = 3092), the total number of actions used during the cracking of each nut (AIC_{Year} = 9452, AIC_{Null} = 9485), and the total number of strikes of the hammer stone performed per nut (AIC_{Year} = 6582, AIC_{Null} = 6617; see Fig. S1 for data on all measured efficiency metrics, including those where we found no effect of aging, and Tables S7-S9 for model summaries for the three metrics which exhibited changes over field seasons).

Whilst all four female chimpanzees took longer to crack nuts in later years, the extent of change varied across individuals from profound changes that are more likely to indicate senescence, to changes that were more likely attributable to small-scale chance fluctuations across nuts (see **Fig. 4**; see Table S10 for model coefficients for each individual). Yo exhibited the largest increase in time between 1999 and 2016 (+28.4 s; difference between 1999 and 2016 = +104%; see supplementary materials for an additional dataset for the duration of nut cracking behaviors performed by Yo in 2018, and corresponding analysis, which demonstrates that Yo took longer to crack oil-palm nuts at an even older age), and Velu exhibited the second largest increase in total time taken to crack oil-palm nuts (+26.5 s; +158%). Jire exhibited a more moderate increase in time taken to crack oil-palm nuts during the same timeframe (+9.7 s; +79%), followed by Fana, who exhibited the smallest change across all females (+5.7 s; +52%). For Fana, it is unclear whether this change represents chance fluctuations, given such small changes in nut cracking duration. Tua, the adult male, exhibited little evidence of a change in oil-palm nut cracking duration across field seasons, with his mean duration of oil-palm nut cracking decreasing by 0.67 s by 2008 (the latest year Tua was observed cracking oil-palm nuts).

Between 1999 and 2016, the median number of actions Yo used to crack and process each oil-palm nut increased (+14 actions per nut; +108% change between 1999 and 2016), as did the median number of times Yo struck each nut with the hammer stone (+8 strikes per nut; +200% change between years). By analyzing the composition of Yo's action repertoire between 1999 and 2016, we determined that, in addition to more striking actions, Yo peeled shell away from kernels using her teeth more frequently in later years (peelteeth SHELL = +6.78% of the total action repertoire composition) and also consumed all kernel in a greater number of bites (eat KERNEL = +5.16% change in total action repertoire composition). Similarly, Velu exhibited an increase in the median number of actions used to crack and process each nut between 1999 and 2016, though this effect

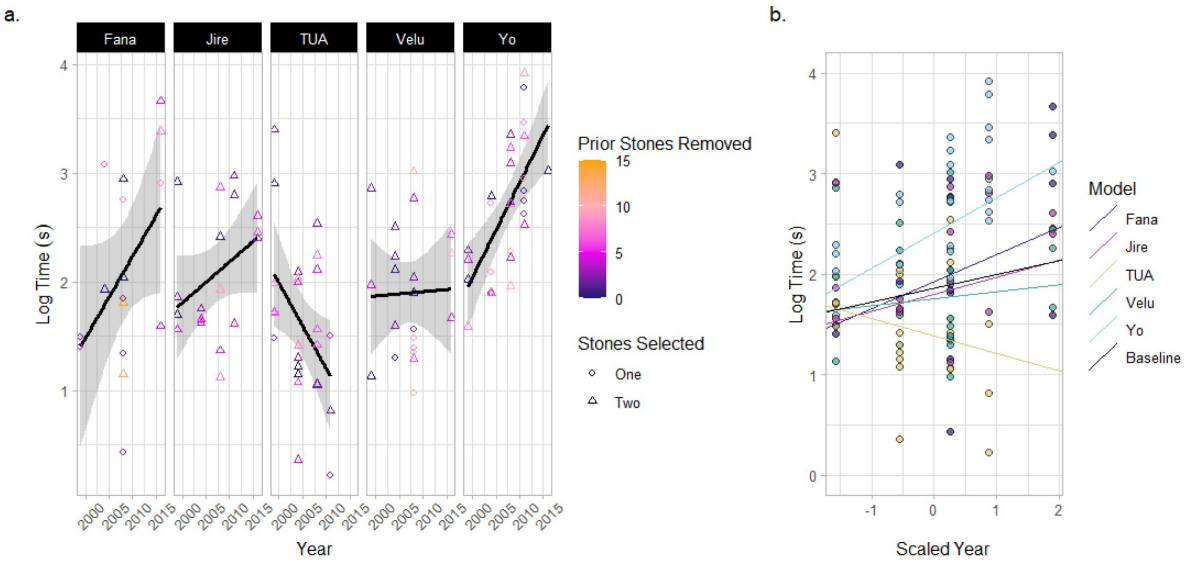

Figure 3.

Duration of stone-tool selection events.

(a) Tool-selection duration times for each old-aged individual. Color correlates with the number of stone tools removed from the matrix prior to that particular tool-selection event. Shape indicates the number of tools selected by an individual in a given tool-selection event. The lines and shaded areas represent a smoothed linear relationship describing the data for each individual. **(b)** A mixed effect model describing the duration of stone tool-selection events across a scaled parameter of the year for each field season. Individuals are included in the model as both a random intercept and slope. Plot shows the model's prediction of the relationship between the duration of stone-tool selection and year for each individual, compared with the baseline fixed effect of year.

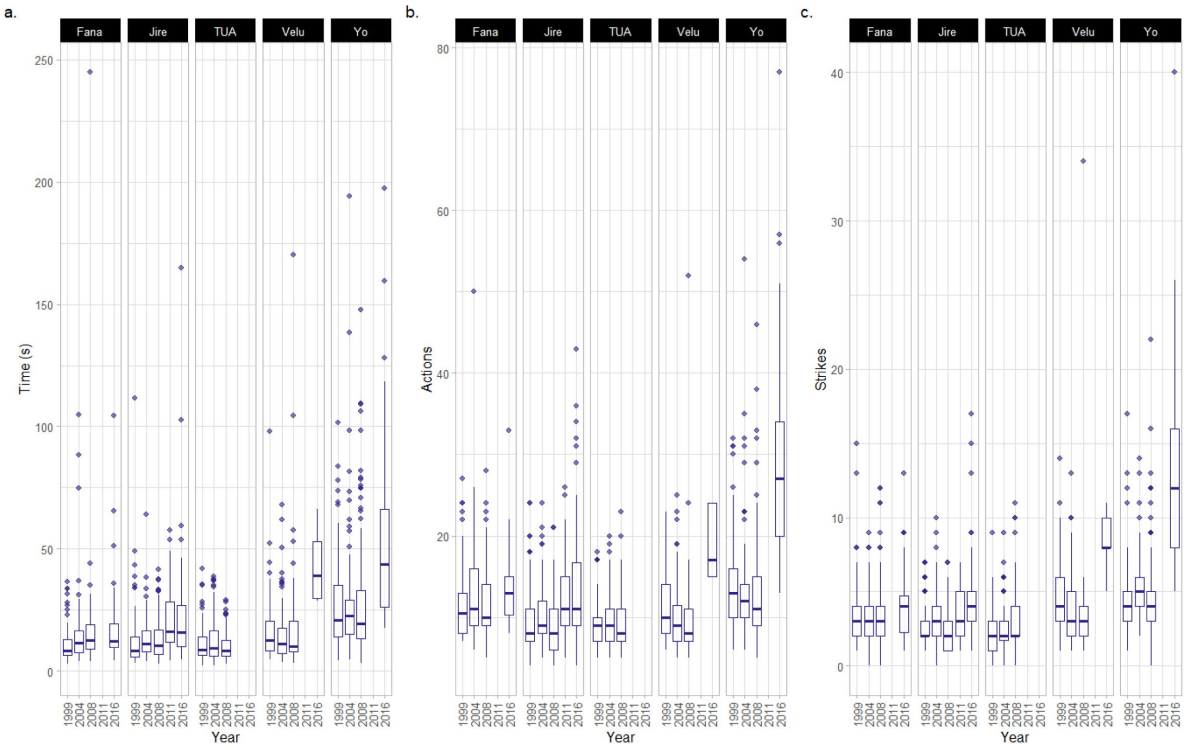

Figure 4.

Metrics of efficiency for the cracking and processing of oil-palm nuts.

This plot only includes metrics in which random slope models outperformed corresponding null models. All data relate to the cracking and processing of individual oil-palm nuts. These metrics include, for each nut cracked, (a) the total time taken (b) the number of discrete actions, and (c) the number of hammer strikes.

was milder (+7 actions; +70% change between 1999 and 2016). For Velu, the majority of these additional actions were strikes of the hammer stone (+4 strikes; +100%). For Fana and Jire, we detected a smaller change in the median number of actions used to crack open oil-palm nuts by 2016 (Fana = +2.5 actions; Jire = +3 actions); however, given that these changes are small, it is more difficult to rule out the possibility that they are due to chance fluctuations in samples between years. Additionally, for Fana and Jire, the median number of striking actions performed per nut in 1999 and 2016 were very similar (Jire: +2 strikes; Fana +1 strike). We found no evidence of Tua performing more or fewer actions when cracking oil-palm nuts (including hammer strikes) over field seasons.

3. Discussion

We provide the first account of how a tool-use behavior performed by wild chimpanzees changed with progressively older age. Across a seventeen-year window, during which chimpanzees aged from 39-44 to 56-61 years old, elderly chimpanzees began visiting experimental nut cracking sites less frequently. This change in attendance rate was not observed for younger chimpanzees, and was therefore confined to individuals who were approaching their maximum age in the wild. In addition, when present at nut cracking sites, two individuals (Fana & Velu) exhibited a lower engagement with nuts and stone tools in 2011 (the latest field season for this analysis) as compared with their behavior in earlier field seasons. With progressive aging, three individuals took longer to select stone tools (Yo, Fana & Jire), several individuals took longer to crack open oil-palm nuts and consume all of the kernel, and two individuals (Yo and Velu) cracked and processed oil-palm nuts using a greater number of actions, including more frequent strikes of the hammer stone. Across metrics of engagement and efficiency, we detected interindividual differences in the extent to which nut cracking behaviors changed with progressive aging, including some individuals who exhibited little-to-no change in behavior across the time period sampled. Overall, our results provide initial evidence that elderly wild chimpanzees are subject to variable effects of aging on their habitual stone tool-use behaviors.

Whilst the outdoor laboratory locations are experimentally-created nut-cracking sites, previous research on the performance of nut cracking across the home range at Bossou established that chimpanzees visit the outdoor laboratory at rates comparable to naturally-occurring sites[64], meaning that for most individuals at Bossou, the outdoor laboratory is a readily-visited site for foraging. However, at progressively older ages, elderly chimpanzees began to visit the outdoor laboratory less frequently. This result was not found for younger chimpanzees between the ages of 8 and 30 years old, suggesting that changes in elderly chimpanzees' attendance rates were not an artefact of environmental changes over field seasons (which would likely affect both age cohorts similarly).

In addition, by 2011, two elderly chimpanzees (Velu & Fana) engaged with nuts and stone tools less frequently than they had done during visits to the outdoor laboratory throughout earlier years (though note for Velu, data for 2011 were collected from a single encounter). The possible causes for these changes in attendance rate – and engagement with nuts and stone tools when present at the outdoor laboratory - are manifold. Firstly, physiological changes with aging – such as in metabolism and nutrient requirements – could influence individuals' dietary preferences, reducing the appeal of nuts as an available food source. Secondly, physical senescence may make visiting nut cracking sites more challenging for elderly individuals, such as through reduced capacity for locomotion. Changes in locomotion have been documented in aging captive apes[18]. In the context of wild apes, reduced mobility may further restrict the available area that elderly chimpanzees can traverse during daily ranging, encouraging them to visit foraging patches that are more proximal to their immediate locations than the outdoor laboratory. Chimpanzees habitually plan their routes towards tool-use sites[64]; however, the extent to which their doing so changes during old age is unclear. Thirdly, it is possible that tool use may become more

challenging due to changes in elderly chimpanzees' cognitive or physical condition (see latter sections of our discussion), which may reduce the appeal of visiting nut cracking sites. Fourthly, changes in social association may have influenced the likelihood that elderly chimpanzees visited experimental nut cracking sites. When experiencing increasingly old ages, many primates[18,25,29,65,66] – and other mammals[67–69] – display higher social selectivity, and spend a greater proportion of their time either in isolation or in smaller group associations. This social aging arguably may not be senescence *per se*, but can either be the result of senescent processes (perhaps even exacerbating senescence[67]), or may act to benefit individuals experiencing senescence, such as reducing the risk of injury from antagonistic interactions with social partners, or by shielding oneself from contagious disease[27,67]. In the context of our study, chimpanzees at Bossou typically arrive at the outdoor laboratory when travelling in groups, and therefore party members may be led to nut cracking sites by associated conspecifics, rather than through independent choice. Previous research has demonstrated that whilst gregariousness appears to be constant across ages in the Bossou chimpanzees[70], two old-aged individuals became notably peripheral in social networks constructed using data from the 2011 field season[71] (Yo and Velu; the two individuals we identified as having the lowest attendance rates), indicating that they were more often seen arriving at the outdoor laboratory alone or travelling as a pair. In tandem with the profound reduction in population size at Bossou throughout our study period[72], changes in social structure may have disproportionately affected elderly chimpanzees, leading to a lower likelihood of visiting the outdoor laboratory alongside – or to regroup with – other community members. Further research is required to link our observed changes in nut cracking engagement to their underlying causes.

Through the collection of longitudinal behavioral data, we were able to evaluate whether at older ages, chimpanzees perform less streamlined tool-use behaviors. At Bossou, chimpanzees exhibit interindividual variation in nut cracking efficiency; however, within-individual efficiency is stable over the majority of each chimpanzees' lifetime[57]. To assess for aging effects, we therefore compared behavior in middle and later adulthood for each chimpanzee, permitting signals of aging to be identified using individually-bespoke baselines of efficiency. Focal chimpanzees exhibited high efficiency in the first field season (1999) suggesting that we began sampling data before the onset of tool-use senescence (see Biro et al. 2003 for data on striking efficiency of adults at Bossou[73], where all adults use approximately 2-4 strikes per oil-palm nut – our focal subset of adults fell within this range in 1999). Of the five individuals included in our study, three individuals took longer to select stone tools over progressing field seasons (Yo, Fana & Jire), two females showed very small increases in the amount of time taken to crack and process nuts (Fana & Jire), whereas two other females exhibited comparatively dramatic increases in the time taken to crack and process each nut (Yo & Velu). Yo and Velu also exhibited more frequent striking using the hammer stone, and Yo performed additional actions to peel shell away from kernels with her mouth, and consumed kernels with a greater number of bites (see Supplementary Video 1 for footage of Yo cracking oil-palm nuts in 1999 and 2016). Our results therefore suggest that there is measurable interindividual variation in the effects of extreme aging on the efficiency of tool selection and use in wild chimpanzees.

Our findings mirror reports of interindividual variability in the senescence of cognitive and physiological systems in both captive and wild primates[19,21,43,74,75]. Whilst it is outside of the scope of our study to determine the precise cognitive, physical, and resultant motivational changes that led to reductions in engagement with tools, rates of tool selection, and the efficiency of tool use, our results can generate predictions about how changes in fine-scale processes may translate into the behavioral changes we have observed with progressive aging. For the chimpanzees that experienced reductions in nut cracking efficiency (as discussed above), these changes could be due to changes in physical strength and dexterity[15,43], visual acuity[23], dentition (where tooth decay may render peeling and chewing actions more difficult[15,76]), or possibly due to changes in cognition relevant to effective tool use[10,12], such as executive functioning or working memory. Changes in tool use behavior may also have emerged to actively

compensate for the effects of senescence that are not in themselves specific to tool use; for example, tooth wear, and subsequent periodontal disease, is common in old-aged chimpanzees[15,76]. The additional strikes of the hammer stone performed by Yo and Velu to crack oil-palm nuts may have therefore been motivated by the desire to break the kernel into a greater number of smaller pieces, which were easier to peel and consume. This conclusion is somewhat supported by post-mortem data for Velu following her death in 2017, as she exhibited heavy wear patterns on both incisors and premolars, and was missing several molars on the lower jaw[77]. Similarly to tool-using efficiency, the duration of tool selection may have taken longer for several individuals due to difficulties identifying the properties of available stones, perhaps due to changes in perceptual systems (such as poorer vision[23]), or cognitive challenges in predicting the properties of objects. Alternatively, longer tool-selection times could have also been due to the need for chimpanzees to weigh up the benefits of specific tool properties (e.g. weight and size), relative to age-related changes in their physical strength and mobility.

Bridging the gap between age-related changes in tool-use behavior, and changes in cognitive and physiological processes, requires further study, and would likely benefit from experimental approaches where possible.

Our study used longitudinal video data collected from a unique, decades-long systematic study of wild chimpanzee tool use, and this video archive likely represents the only currently available data source to study intraindividual variation in chimpanzee nut cracking across the span of decades[57]. Moreover, given the exceptionally long lives of several chimpanzees at Bossou[78], Bossou represents a unique population whose individuals can be readily studied to examine the effects of senescence in the wild at the level of the individual. However, the use of existing video data, and time-intensive methods for fine-scaled behavior coding, means that our study faced a number of limitations.

Firstly, we were unable to analyze whether specific ecological variables – such as the availability of different food sources, and demographic changes at Bossou – influence aging individuals' attendance at the outdoor laboratory, as well as at naturally-occurring nut cracking sites (see discussion above). Nevertheless, by using the attendance of younger individuals as a control, we were able to identify that the reduction in attendance over field seasons was limited to older individuals, suggesting a specific change in behavior associated with chimpanzees experiencing progressively old age. Further research is needed to understand what factors lead to this reduced engagement with nut cracking at older ages, how aging individuals compensate for calorie loss from reduced nut cracking, and more generally, how aging influences chimpanzees' foraging behaviors across their entire home range.

Secondly, we were not able to eliminate all possible ecological explanations for age-related changes in tool-using efficiency[79,80]. Some ecological variables were controlled for as part of the experimental set up at the outdoor laboratory. For example, chimpanzees were always tested during similar months of the year in each field season, and were provided with oil-palm nuts at a suitable stage of maturity (and thus of similar hardness). Previous studies at Bossou have also revealed that chimpanzees are able to select nuts that are suitable for cracking, further suggesting that chimpanzees can account for differences in nut quality during tool use[81] (though this could also have been affected by aging itself, such as through reduced visual acuity impeding suitable nut selection[23]). Whilst it is possible that other ecological factors may influence our results, we believe that inter-seasonal ecological differences are unlikely to fully explain them. Firstly, if differences in chimpanzees' nut cracking efficiency between seasons was being driven by ecological variation, we predict that this inter-annual variation would be equally present across early and late field seasons. However, contrary to this prediction, nut-cracking efficiency was very similar across early field seasons (and across individuals during these years); changes in efficiency were only detected in later field seasons, when chimpanzees were sampled at older ages. Secondly, if inter-annual differences in ecology rendered nut cracking more difficult in later field seasons,

we would expect these ecological changes to affect all individuals similarly. This was also not the case, as changes in behavior differed between individuals – some maintained similar levels of efficiency (such as Fana), whereas other individuals experienced profound reductions in efficiency (such as Velu and Yo). For Yo (the individual with the greatest reduction in tool-using efficiency) the observations that Yo took even longer to crack oil-palm nuts in 2018, (and that Yo also struggled to crack coula nuts in 2011, see supplementary materials for further information) provide evidence for a directional, individual-specific reduction in nut-cracking efficiency across later years, rather than her efficiency being dictated by ecological variation. We could not provide data on a cohort of younger adults cracking nuts across field seasons, as there was only one young adult (male) individual at Bossou between 1999-2016. An additional younger adult cohort would have been a desirable control group for our study, to complement our long-term efficiency baselines we provide at the level of the individual. For future studies, we believe that the collection of a wider array of ecological data would be valuable for discriminating between explanations with greater confidence and, where possible, future studies should aim to collect long-term data on the behavior of younger adults as additional control groups.

Thirdly, as data were collected from video footage, we could not examine how the dimensions of tools and raw material types influenced chimpanzees' tool-use behaviors over different encounters, and across field seasons. Throughout long-term data collection at Bossou, the stone tools available at the outdoor laboratory have been kept as consistent as possible, and chimpanzees select tools with physical properties which likely enhance nut cracking efficiency[32,63]. Indeed, changes in tool-using efficiency may be borne from increasing difficulty selecting appropriate tools with aging. Future studies should gather data on tool properties to support analyses of aging effects in tool use. These studies could be combined with data collection on even more fined grained behaviors of apes when using tools, such as the specific grips used to manipulate objects over time[82,83].

Fourthly, our study was limited to a small sample size of five aging chimpanzees. This is an inevitability of collecting longitudinal data on long-lived wild individuals who are approaching the ends of their lifespan. Further data is needed – including from other field sites – to establish whether the variation in aging effects we have found generalize to other individuals and populations (and, where possible, other tool use behaviors).

Much like human technical skills, the tool-use behaviors of chimpanzees and other great apes are culturally-variable behaviors that are acquired through a mixture of social learning and individual practice[44,56,73,84]. As previously mentioned, prior research on nut cracking behavior at Bossou has revealed that chimpanzees vary in the age of skill acquisition[44,56], and the efficiency with which nut cracking is performed across adulthood varies between individuals, yet is stable within individuals over time[57]. These differences in individual performance are, in part, likely due to differences in the environments of learners during skill acquisition[85]. Our results expand on these findings to highlight that, whilst chimpanzees at Bossou perform nut cracking behaviors throughout their lives (suggesting that this is an important skill for this population), progressive aging and senescence may exaggerate interindividual differences in the performance of socially-learnt skills, as seen in humans[86,87]. Taken as a whole, our results provide further evidence that the cultural behaviors of humans and chimpanzees exhibit marked similarities that extend across their lifetimes including, for some individuals, a period of technological senescence that can manifest across the oldest years of life. Further research should examine whether similar factors influence senescence of technical skills between humans and apes. This research should include studies that determine whether skill proficiency in early life and adulthood, and the frequency with which skills continue to be performed in later life, influence the rate and likelihood of senescence. Furthermore, debate continues as to whether human behaviors are particularly susceptible to the effects of aging due to the development of neurodegenerative diseases, such as Alzheimer's and Parkinson's disease[2,62,88,89]. Current evidence suggests that the effects of these neurological changes in humans have far more

profound impacts on behavior, despite aging primates sometimes exhibiting similar neuropathological signatures of aging[5,90–92]. Yet, it is still not clear whether this conclusion comes from a lack of behavioral data on aging in primates. We were not able to collect neurological samples from the chimpanzees in our study, and cannot say whether the changes we observed could be associated with such processes (including for Yo, whose more profound senescence renders her the most likely to suffer from neurological decline). However, tool use could offer a suitable domain in which to examine the possible manifestation of such diseases (if present). Field sites should make specific efforts to collect long-term data on behavioral changes with aging – including for tool-use – and where possible aim to sample neurological data following the natural deaths of wild, elderly individuals. These data will provide important insights into the underlying causes of human and chimpanzee skill disruption in the contexts of healthy and diseased aging.

In foraging contexts, multi-object tool-use behaviors are often used to extract energy-rich resources that would not be otherwise accessible[93]. Given the sample size of our study, and limitations in the wider ecological data available, it was not possible to identify the influence of tool-use senescence on individual survivability through reduced energy intake. Answering this question would require data on a greater number of tool-use behaviors, spanning across the home-range. However, the two females in our study who exhibited limited changes in tool-using efficiency (Jire & Fana) had the longest lifespan after the end of our study, whereas Velu and Yo (who experienced greater difficulty cracking nuts in later years) died comparatively shortly after our sample period. While this sample is too small to make strong claims, this pattern could indicate that the senescence of tool-use behaviors, and the energy-rich foods to which they permit access, can contribute to reduced survivability in the wild. Alternatively, changes in tool-use behaviors could offer a litmus for identifying individuals experiencing profound generalized senescence in the wild, where changes in many physiological and behavioral processes subsequently impact an individual's survivability. By extension, outside of tool use, our data on individual survivability – alongside previous studies of chimpanzees at Bossou – invites speculation surrounding whether the social relationships of specific individuals may reduce or accentuate the rate and intensity of senescence with progressive aging. In addition to living for a longer period after the final field season we sampled, Fana and Jire enjoyed more central social positions than other elderly females at Bossou[71], and had a greater number of living relatives during the latter field seasons (during which Jire had two mature offspring, and Fana had two mature offspring, and two young grandchildren). Given that only eight individuals remained at Bossou by 2016, these familial relationships constituted a significant proportion of the overall community. Further research will provide insight into if and how lifetime sociality and familial success influences the onset and rate of senescence in wild chimpanzees, for example through socially-mediated resource acquisition.

In sum, we demonstrate that the tool-use behaviors of wild chimpanzees can change in old age, and that these changes vary between individuals. Whilst our study is observational, we argue that processes of senescence offer a promising explanation for such changes, particularly in regard to changes in individual tool-using efficiency. Our findings reflect the conclusions of previous studies investigating the cognitive and physiological senescence of primates living in captivity, and generate a myriad of further questions about the possible underlying mechanisms of tool-use senescence, as well as more general behavioral aging in wild apes. As questions surrounding aging benefit from longitudinal data – which for many primates require collection across decades – the possibility that such questions will be answered is becoming increasingly more precarious in an age where primates are at a heightened risk of extinction[94]. The conservation of wild primate populations is paramount for our understanding the dynamics and evolution of primate aging processes, which may reveal insights into the forces influencing behavioral stability and senescence across the human lifetime.

4. Methods

4.1 Study site and video archive

Established in 1976, Bossou (07° 390' N; 008° 300' W) is a site of long-term research focused on a small population of wild West-African chimpanzees[44]. Chimpanzees at Bossou possess an extensive repertoire of tool-use behaviors[95], including nut cracking[32,47,55,73]. For many years, the size of the Bossou chimpanzee community remained relatively stable at around 20 individuals; however, following a flu-like epidemic in 2002 that killed 5 individuals[72], the population began an irrecoverable decline. At the time of writing (2024), the Bossou community consists of just three individuals.

Nut cracking by Bossou chimpanzees has been studied for several decades through the use of an 'outdoor laboratory'[47] (established in 1988; see **Fig. 1**). Open during the dry season of each year (approx. November-February), the outdoor laboratory is a maintained natural clearing in the forest (approx. 7 x 20 m) where nuts and stones are provided for chimpanzees. These typically consist of oil-palm nuts, *Elaeis guineensis,* which is the only species that occurs naturally at Bossou and thus the only species of nut habitually cracked by these chimpanzees. Oil-palm nuts were sourced from local communities surrounding Bossou, and nuts provided to chimpanzees were generally of suitable maturity for cracking and consumption. In some years, coula nuts, *Coula edulis,* and in one-year panda nuts, *Panda oleosa*, were also provided. Neither coula nor panda nuts occur naturally at Bossou, but both are cracked by chimpanzees at nearby sites[73]. In addition to nuts, chimpanzees are also provided with over 50 stones organized in a square matrix in the center of the clearing at the start of each session (see **Fig. 1d**), as well as a raceme of edible oil-palm fruits (see **Fig. 1c**). The outdoor laboratory also features a water point (a hollowed section of a tree trunk; see **Fig. 1b**) from which chimpanzees may extract water for drinking using leaf tools. Chimpanzees visit the outdoor laboratory spontaneously as part of their daily ranging behaviors, and with comparable frequency to other naturally-occurring nut cracking sites within the home range at Bossou[64]. Upon arrival at the outdoor laboratory, chimpanzees' behaviors are recorded by observers using 2 or 3 video cameras located behind a screen of vegetation.

Video data collected at the outdoor laboratory has recently been collated into a longitudinal archive spanning from 1990 to the present day[57,71,96]. Given the long-term use of the outdoor laboratory to study nut cracking, all chimpanzees were well habituated to the experimental set up by 1999 (the first field season from which data was sampled for this study). The Bossou archive also contains data on the composition of all recorded encounters with groups of chimpanzees at the outdoor laboratory across this timeframe, and can be combined with recorded family lineage data (including birth data for individuals born after the establishment of long-term research at Bossou). The Bossou archive therefore presents a novel opportunity for longitudinal analysis of whether and how tool-use behaviors change across the later periods of chimpanzee lifespans.

We collected and analyzed data on the behaviors of chimpanzees at the outdoor laboratory at Bossou, spanning a seventeen-year period (1999-2016). This 17-year period contains the majority of the available video data collected at Bossou. To balance fine-grained behavior coding (which is highly time intensive) with the need to sample data over an extended time period to capture possible effects of long-term senescence, we aimed to sample field seasons within this time window at four-year intervals; however, in some years, data was not collected at Bossou (such as during years where disease outbreaks were affecting local communities). In such instances, we sampled the closest field season which likely contained sufficient data for our analyses. Thus, during this period, we sampled data from five field seasons (1999, 2004, 2008, 2011, and 2016).

Over the years, the outdoor laboratory has operated at two locations in the forest. Between 1999 and 2008, data was only collected at one specific location across the years. However, in 2011 a second clearing was made available to chimpanzees, with an identical experimental set up. In 2011, data was collected in both locations simultaneously. By 2016, all data collection had transitioned to the newer, second location. For the majority of our analyses, we therefore used data from the first location between the years of 1999-2011, and the second location in 2016. For only one analysis (attendance rate, see below) we used data from both the first and second outdoor laboratory location in 2011. All behavior coding in our study was performed using the open-access software BORIS[97], with videos viewed on a 59cm monitor.

4.2 Attendance

We recorded the total number of times chimpanzees were encountered at the outdoor laboratory in each field season. An encounter was defined as any instance where one or a group of chimpanzees visited the outdoor laboratory, and lasted until all chimpanzees left. If a chimpanzee left the outdoor laboratory and returned before all other individuals had left, it was classed as part of the same encounter. We collected data on the five chimpanzees experiencing increasingly old age, as well as for an additional cohort of all adult and subadult individuals between the ages of 8 and 30 years old. This second cohort of individuals allowed us to evaluate whether changes in attendance rate over progressive field seasons may be due to confounding factors other than senescence, such as changes in environmental food availability or population structure, or changes in the number of experimental nut cracking sites. For our younger cohort of chimpanzees, we used a minimum age of 8 years old, as chimpanzees at Bossou acquire the skill of nut cracking by 7 years of age. For this analysis, we also excluded two adult females (Pama and Nina) who never learnt to successfully crack nuts using stone tools. To evaluate whether progressive aging reduced attendance rates, we constructed a Poisson GLMM with field season as a continuous fixed effect (scaled about the mean), and cohort (above or below 30 years) as a categorical variable. Rates of attendance were estimated using encounters (a count variable) and the inclusion of an offset term in our model (the number of days of the field season). Importantly, we included an interaction term in our model to see whether the relationship between aging across field seasons and attendance rate was more severe for our focal elderly individuals compared with the younger cohort. Individual ID was included as a random intercept to account for repeated measures of the same individual across field seasons.

4.3 Behaviors at the outdoor laboratory

We estimated whether, over successive field seasons, elderly individuals began spending a greater or lesser proportion of their time engaging in nut cracking when present at the outdoor laboratory, as compared with other commonly performed behaviors. For each elderly individual, we sampled the first 10 encounters of each field season in which they were present (totaling a maximum of 50 encounters per individual across all field seasons). For each encounter, we timed how long individuals engaged in one of four mutually exclusive categories of behavior:

1. **Engaging with Nuts and Stone Tools**: the total amount of time individuals spent interacting with nuts, nut fragments (including shells and kernels), and stones. Coding began when an individual first touched a nut, nut fragment, or stone.
2. **Drinking Water**: the total amount of time individuals spent producing leaf tools and drinking from the water point. Coding began when an individual stripped leaves from branches to begin manufacturing a leaf tool to aid in drinking water, or, if reusing a tool that had previously been made and discarded, when they collected the tool, and began to approach the water point to drink.
3. **Eating Oil-Palm Fruits**: the total amount of time individuals spent consuming oil-palm fruits from the raceme. Coding began whenever an individual started picking oil-palm fruits from the raceme, or collecting and consuming oil-palm fruits off of the ground.
4. **Other**: any other behaviors (e.g. grooming, playing, resting).

For behaviors 1-3, coding ceased when individuals stopped interacting with all relevant objects of one behavior (e.g. leaf tools, stones, fruits), and began engaging in another behavior (either another behavior from 1-3, or 'Other' behaviors such as grooming). If an individual dropped all relevant items and was idle for at least one minute, they were considered to be resting, and behaviors were marked as 'Other'. For field seasons in which individuals did not visit the outdoor laboratory on at least 10 occasions, all available encounters were used. We also recorded the total amount of time each focal individual spent at the outdoor laboratory during each encounter. We calculated the proportion of time individuals spent engaging in each type of behavior across all encounters of each field season (thus, controlling for differences in the total time individuals were observed between years). For this analysis, we omitted any videos collected at the second outdoor laboratory site (including some videos from 2011 and all videos from 2016). We chose to do so as the two sites vary in how accessible they are (with the original site being situated at the top of a steep hill, but the second requiring no climb). This difference in terrain may influence the behaviors of the chimpanzees once arriving at the outdoor laboratory, for example, more time resting following climbing.

4.4 Stone-tool selection

We measured the time taken for the old-aged chimpanzees to select stone tools at the central matrix during each of the sampled field seasons. We sampled the first 10 encounters with each individual for each field season. All tool-selection events in these encounters were sampled. We began timing when chimpanzees approached the matrix and we considered their gaze to be fixed on at least one stone tool. We stopped timing when chimpanzees turned away from the matrix holding all acquired stone tools. We recorded the number of stone tools taken by the focal chimpanzee during each instance of stone-tool selection (a categorical score of 'one' or 'two' stones). Additionally, we recorded the number of stone tools that had been removed from the stone-tool matrix prior to each stone selection event (including those removed by other individuals, as well as the focal chimpanzee during previous instances of stone-tool selection). We could therefore incorporate into our analysis a metric of how many options were available to chimpanzees during each stone-tool selection event (where higher numbers of previously selected tools indicated a smaller pool of possible choices). We did not sample instances where chimpanzees selected and used tools which were not positioned at the central matrix (i.e. when using tools which had already been transported away from the matrix by other chimpanzees). When modelling tool-selection time over field seasons, both the number of stones that a chimpanzee selected from the central matrix (one or two) and the number of stones previously removed from the matrix were included in our model as fixed effects, to control for additional variation in selection time introduced by these two factors (see section 4.6 below for more details on GLMM model structures).

4.5 Coding discrete actions

When performing complex technical skills—including tool-use behaviors— experienced apes organize individual actions into more streamlined goal-directed sequences[30,33,56,98], and begin to successfully perform behaviors more quickly[33,37,73,82]; however, whether experiencing progressively old age influences this efficiency has not yet been studied.

To evaluate the efficiency with which focal chimpanzees engaged in nut cracking, we coded the individual, fine-grained actions used by focal chimpanzees when cracking nuts at the outdoor laboratories. We sampled videos chronologically from each sampled field season. Fine-grained action coding was conducted for each individual in each field season until at least 1000 actions had been collected, and included sequences of actions that described the cracking of at least 20 nuts in their entirety. To code sequences of actions, we used an ethogram of 34 manipulations (e.g. 'Grasp', 'Drop', 'Strike') and 6 objects (see Table S1 for full ethogram[33]; all discrete-action coding was performed by one individual: EHS; our ethogram was tested to ensure that it can be applied objectively as part of a previous research project[33]). The six possible objects included: Hammer,

Anvil, Nut, Kernel (the edible interior of a nut), Shell (the inedible exterior of a nut), and Bare Hand (for use when individuals performed an action in the absence of an object, e.g., striking the anvil with bare hand). Stone tools were categorized as 'Hammer' or 'Anvil' based on how they were used by the individual. If an individual swapped over their hammer and anvil stones, the stones were reassigned accordingly. Thus, stone tools were coded according to their function at any specific point in a sequence. We considered an individual action to be the combination of both the manipulation performed by the chimpanzee, and the object being manipulated (e.g. 'Grasp Hammer' = one action).

Coding of action sequences started when an individual began interacting with a nut, nut fragment, or stone, and ceased when an individual dropped all relevant objects and either began engaging in an alternative behavior (e.g. grooming, feeding on oil-palm fruits, etc.) or rested for longer than one minute. Actions were coded as discrete events during behavioral observation, and the time of each action was automatically recorded in BORIS.

The total corpus of actions was parsed into sequences directed at the cracking of individual nuts and the consumption of all associated kernel. Only sequences which described the entire processing of a nut, from acquisition of the nut to complete consumption of the kernel, were included in our analysis. A number of metrics of efficiency were extracted from action sequences directed at individual nuts, which emphasize the speed with which kernels can be acquired and consumed, and the extent to which the actions used to do so reflect a streamlined behavioral sequence:

1. **Total time to crack nuts and consume all kernel.** The total time between the start of the first action and the end of the last action performed on a specific nut, including all actions involving the consumption of kernel, and disposal of shell fragments.
2. **Number of actions used to process nuts and consume all kernel.** The total number of actions performed during the cracking of a specific nut, including consumption of kernel and disposal of shell fragments.
3. **Number of unique types of action used to process nuts and consume all kernel.** The number of different types of actions performed by an individual when cracking a specific nut, including all kernel consumption and disposal of shell fragments. This metric is different to [2] as it describes the variety of actions employed, rather than the number; e.g. for the action sequence *A*,*A*,*B*,*C*,*B*,*C*, where letters denote hypothetical actions, the number of actions is six, and the number of unique action types is three {*A*, *B*, *C*}.
4. **Number of times the nut was (re)placed on the anvil**. The number of times the nut was placed on the anvil during initial placement, and also all replacements when the nut rolled off the anvil. An understanding of how to orient the anvil, and where to place the nut can reduce the likelihood of needing to perform nut replacements. Therefore, fewer nut placements reflects a greater efficiency in nut cracking.
5. **Number of strikes of the hammer stone per nut.** The number of individual strikes of the hammer stone performed on each nut that a chimpanzee cracked. This is a common metric for efficiency in chimpanzee nut cracking[73,99], where fewer strikes indicate higher efficiency.
6. **Number of tool reorientations per nut.** The total number of horizontal rotations ('reorient') and vertical rotations ('flip') of hammer and anvil stones. Chimpanzees occasionally reorient tools during tool use, with these adjustments likely reflecting attempts to achieve greater efficiency. Once a suitable configuration of tool objects is acquired, such reorientations are usually less common.
7. **Tool changes per nut.** The number of times an individual swapped over their hammer and anvil stones, swapped out at least one stone tool for a new stone, or moved across the outdoor laboratory to use a hammer-anvil set previously abandoned by another user.

4.6 Statistical analyses

Statistical analyses were performed in R (version 4.3.3 Angel Food Cake). For attendance rates, tool-selection times, and the metrics of efficiency cracking individual nuts, we used linear and generalized linear mixed-effect models to assess for the effects of age (using the lme4 package[100]). Linear mixed effect models were used in any instance where time was a response variable (time was logged to confer normality); whereas, if a response variable was measured in counts (e.g., number of actions used to crack open a nut; number of encounters over a field season, etc.), we employed generalized linear mixed-effect models using a Poisson distribution. In both instances, year of the field season (scaled about the mean) was used as a fixed effect, as a proxy for age.

Our model for attendance data is described above in section 4.2 (we describe this model separately as we modelled the effect of aging in two separate groups – young and old – rather than for specific individuals). For all other metrics, we modelled the effect of aging on focal, elderly chimpanzees by using random intercepts and slopes to evaluate the effect of the increasing year of each field season. Our decision to include a random slope is supported by previous research on captive and wild primates, which suggests that the effects of senescence are highly variable across individuals for a number of physiological and cognitive processes[19,21,43,74,75]. Across metrics of engagement and efficiency, we compared random-slope models with fixed slope models - which assume that the effect of increasing field season will be the same for all individuals - as well as with null models which fit an intercept across all field seasons (and therefore assumed no effect of aging). This allowed us to evaluate whether the effect of increasing year of each field season influenced chimpanzee behavior, and also whether this effect was variable across individuals. All model comparisons were performed using AIC, where lower scores indicate better fit relative to model complexity. Where necessary, we also included the specific encounter as an additional random intercept (fixed slope) to avoid pseudoreplication from multiple tool-selection events within the same encounter.

When analyzing metrics of nut cracking efficiency (for which we had a total of seven metrics, see above), we restricted the use of models to describe changes in metrics based on whether, for at least one individual, the median value for a particular field season fell outside the interquartile range of any previous field season. If a model identified that an efficiency metric was changing across field seasons, we used model coefficients to gauge the direction of change for each individual. To estimate the magnitude of change across field seasons, we compared data collected for each individual in the earliest and latest year that they were sampled. We calculated % change as the change in a metric between the last and first field season, divided by the value for the first field season (to scale the change), multiplied by 100 (see associated code).

4.7 Ethics Statement

Data collection at Bossou has been conducted by different researchers over several decades. Research authorization and ethical approval were given to T.M. (who oversaw data collection during the study period covered by this project) through a memorandum of understanding between Kyoto University, and the Guinean authorities (Direction Générale de la Recherche Scientifique et de l'Innovation Technologique, DGERSIT, and the Institut de Recherche Environnementale de Bossou, IREB), to which all researchers conformed. The present study was entirely conducted using existing video data from Bossou (the Bossou Archive), and therefore did not involve collection of additional data from wild chimpanzees.

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Additional information

Author Contributions

E.H.S., D.B. and T.G. conceived and designed this project. T.M., D.B., C.H., S.C., and K.A.W. conducted data collection at Bossou, with T.M. leading the Bossou project across the timeframe of data collection relevant to this study. E.H.S. performed all behavior coding from video data collected between 1999-2016, and K.AW collected time-duration data for 2018. D.B. and T.G. supervised this project. E.H.S. analyzed the data and produced all figures. E.H.S. led the writing of this paper, with all authors contributing throughout drafting and revisions. T.G. & D.B. are joint senior authors.

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Data and code availability

All data and code associated with this manuscript can be found at: *https://github.com/Elliot-HS/NutCracking_Senescence*

Additional files

Supplementary_Video_1

Supplementary_Video_2

Supplementary_Materials

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Reviewer #1 (Public review):

Summary:

Howard-Spink et al. investigated how older chimpanzees changed their behavior regarding stone tool use for nutcracking over a period of 17 years, from late adulthood to old age. This behavior is cognitively demanding, and it is a good target for understanding aging in wild primates. They used several factors to follow the aging process of five individuals, from attendance at the nut-cracking outdoor laboratory site to time to select tools and efficiency in nut-cracking to check if older chimpanzee changed their behavior.

Indeed, older chimpanzees reduced their visits to the outdoor lab, which was not observed in the younger adults. The authors discuss several reasons for that; the main ones being physiological changes, cognitive and physical constraints, and changes in social associations. Much of the discussion is hypothetical, but a good starting point, as there is not much information about senescence in wild chimpanzees.

The efficiency for nut-cracking was variable, with some individuals taking a long time to crack nuts while others showed little variance. As this is not compared with the younger individuals and the sample is small (only five individuals), it is difficult to be sure if this is also partly a normal variance caused by other factors (ecology) or is only related to senescence.

Strengths:

(1) 17 years of longitudinal data in the same setting, following the same individuals.

(2) Using stone tool use, a cognitively demanding behavior, to understand the aging process.

Weaknesses:

A lack of comparison of the stone tool use behavior with younger individuals in the same period, to check if the changes observed are only related to age or if it is an overall variance. The comparison with younger chimpanzees was only done for one of the variables (attendance).

Comments on Revised Version (from BRE):

The authors have now added to the manuscript that they did not have sufficient data to compare additional variables to younger chimpanzees, and therefore compared intra-individual variation across field seasons. They have also explained that nut hardness, although not measured, was largely controlled for due to the experimental nature of the 'outdoor laboratory' whereby only nuts of a suitable maturity (and hardness) are provided to the chimpanzees. The discussion now also includes mention of other ecological variables and their potential influence on the results.

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Reviewer #2 (Public review):

Summary:

Primates are a particularly important and oft-applied model for understanding the evolution of, e.g., life history and senescence in humans. Although there is a growing body of work on aging in primates, there are three components of primate senescence research that have been underutilized or understudied: (1) longitudinal datasets, (2) wild populations, and (3) (stone) tool-use behaviors. Therefore, the goal of this study was to (1) use a 17-year longitudinal dataset (2) of wild chimpanzees in the Bossou forest, (3) visiting a site for field experiments on nut-cracking. They sampled and analyzed data from five field seasons for five chimpanzees of old age. From this sample, Howard-Spink and colleagues noted a decline in tool-use and tool-use efficiency in some individuals, but not in others. The authors then conclude that there is a measurable effect of senescence on chimpanzee behavior, but that it varies individually. The study has major intellectual value as a building block for future research, but there are several major caveats.

Strengths:

With this study, Howard-Spink and colleagues make a foray into a neglected topic of research: the impact of the physiological and cognitive changes due to senescence on stone tool use in chimpanzees. Based on novelty alone, this is a valuable study. The authors cleverly make use of a longitudinal record covering 17 years of field data, which provides a window into long-term changes in the behavior of wild chimpanzees, which I agree cannot be understood through cross-sectional comparisons.

The metrics of 'efficiency' (see caveats below) are suitable for measuring changes in technological behavior over time, as specifically tailored to the nut-cracking (e.g., time, number of actions, number of strikes, tool changes). The ethogram and the coding protocol are also suitable for studying the target questions and objectives. I would recommend, however, the inclusion of further variables that will assist in improving the amount of valid data that can be extrapolated (see also below).

With this pilot, Howard-Spink and colleagues have established a foundation upon which future research can be designed, including further investigation with the Bossou dataset and other existing video archives, but especially future targeted data collection, which can be designed to overcome some of the limits and confounds that can be identified in the current study.

Weaknesses:

Although I agree with the reasoning behind conducting this research and understand that, as the authors state, there are logistical considerations that have to be made when planning and executing such a study, there are a number of methodological and theoretical shortcomings that either need to be more explicitly stated by the authors or would require additional data collection and analysis.

One of the main limitations of this study is the small sample size. There are only 5 of the old-aged individuals, which is not enough to draw any inferences about aging for chimpanzees more generally. Howard-Spink and colleagues also study data from only five of the 17 years of recorded data at Bossou. The selection of this subset of data requires clarification: why were these intervals chosen, why this number of data points, and how do we know that it provides a representative picture of the age-related changes of the full 17 years?

With measuring and interpreting the 'efficiency' of behaviors, there are in-built assumptions about the goals of the agents and how we can define efficiency. First, it may be that efficiency is not an intentional goal for nut-cracking at all, but rather, e.g., productivity as far as the number of uncrushed kernels (cf. Putt 2015). Second, what is 'efficient' for the human observer might not be efficient for the chimpanzee who is performing the behavior. More instances of tool-switching may be considered inefficient, but it might also be a valid strategy for extracting more from the nuts, etc. Understanding the goals of chimpanzees may be a difficult proposition, but these are uncertainties that must be kept in mind when interpreting and discussing 'decline' or any change in technological behaviors over time.

For the study of the physiological impact of senescence of tool use (i.e., on strength and coordination), the study would benefit from the inclusion of variables like grip type and (approximate) stone size (Neufuss et al., 2016). The size and shape of stones for nut-cracking have been shown to influence the efficacy and 'efficiency' of tool use (i.e., the same metrics of 'efficiency' implemented by Howard-Spink et al. in the current study), meaning raw material properties are a potential confound that the authors have not evaluated.

Similarly, inter- and intraspecific variation in the properties of nuts being processed is another confound (Falótico et al., 2022; Proffitt et al., 2022). If oil palm nuts were varying year-to-year, for example, this would theoretically have an effect on the behavioral forms and strategies employed by the chimpanzees, and thus, any metric of efficiency being collected and analyzed. Further, it is perplexing that the authors analyze only one year where the coula nuts were provided at the test site, but these were provided during multiple field seasons. It would be more useful to compare data from a similar number of field seasons with both species if we are to study age-related changes in nut processing over time (one season of coula nut-cracking certainly does not achieve this).

Both individual personality (especially neophilia versus neophobia; e.g., Forss & Willems, 2022) and motivation factors (Tennie & Call, 2023) are further confounds that can contribute to a more valid interpretation of the patterns found. To draw any conclusions about age-related changes in diet and food preferences, we would need to have data on the overall food intake/preferences of the individuals and the food availability in the home range. The authors refer briefly to this limitation, but the implications for the interpretation of the data are not sufficiently underlined (e.g., for the relevance of age-related decline in stone tool-use ability for individual survival).

Generally speaking, there is a lack of consideration for temporal variation in ecological factors. As a control for these, Howard-Spink and colleagues have examined behavioral data for younger individuals from Bossou in the same years, to ostensibly show that patterns in older adults are different from patterns in younger adults, which is fair given the available data. Nonetheless, they seem to focus mostly on the start and end points and not patterns that occur in between. For example, there is a curious drop in attendance rate for all individuals in the 2008 season, the implications of which are not discussed by the authors.

As far as attendance, Howard-Spink and colleagues also discuss how this might be explained by changes in social standing in later life (i.e., chimpanzees move to the fringes of the social network and become less likely to visit gathering sites). This is not senescence in the sense of physiological and cognitive decline with older age. Instead, the reduced attendance due to changes in social standing seems rather to exacerbate signs of aging rather than be an indicator of it itself. The authors also mention a flu-like epidemic that caused the death of 5 individuals; the subsequent population decline and related changes in demography also warrant more discussion and characterization in the manuscript.

Understandably, some of these issues cannot be evaluated or corrected with the presented dataset. Nonetheless, these undermine how certain and/or deterministic their conclusions can really be considered. Howard-Spink et al. have not strongly 'demonstrated' the validity of relationships between the variables of the study. If anything, their cursory observations provide us with methods to apply and hypotheses to test in future studies. It is likely that with higher-resolution datasets, the individual variability in age-related decline in tool-use abilities will be replicated. For now, this can be considered a starting point, which will hopefully inspire future attempts to research these questions.

Falótico, T., Valença, T., Verderane, M. & Fogaça, M. D. Stone tools differences across three capuchin monkey populations: food's physical properties, ecology, and culture. Sci. Rep. 12, 14365 (2022).
Forss, S. & Willems, E. The curious case of great ape curiosity and how it is shaped by sociality. Ethology 128, 552-563 (2022).
Neufuss, J., Humle, T., Cremaschi, A. & Kivell, T. L. Nut-cracking behaviour in wild-born, rehabilitated bonobos (Pan paniscus): a comprehensive study of hand-preference, hand grips and efficiency. Am. J. Primatol. 79, e22589 (2016).
Proffitt, T., Reeves, J. S., Pacome, S. S. & Luncz, L. V. Identifying functional and regional differences in chimpanzee stone tool technology. R. Soc. Open Sci. 9, 220826 (2022).
Putt, S. S. The origins of stone tool reduction and the transition to knapping: An experimental approach. J. Archaeol. Sci.: Rep. 2, 51-60 (2015).
Tennie, C. & Call, J. Unmotivated subjects cannot provide interpretable data and tasks with sensitive learning periods require appropriately aged subjects: A Commentary on Koops et al. (2022) "Field experiments find no evidence that chimpanzee nut cracking can be independently innovated". ABC 10, 89-94 (2023).

Comments on Revised Version (from BRE):

The authors have revised their methods to clarify why certain field seasons were chosen and have clarified aspects of their analysis relevant to this reviewer's concerns. The coula nut cracking data and results which were of a single season have now been restricted to the Supplementary. The revised discussion now includes a much more detailed limitations section including both ecological factors but also the effects of social aging. Stone tool size, grip and other factors are also acknowledged as being potentially important for measuring efficiency but the authors were unable to include in this study due to the nature of the dataset.

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Author response:

The following is the authors' response to the original reviews

The main criticisms levied by both reviewers can be traced down to our use of a long-term video archive to assess for the effects of aging on individual chimpanzees over extended time periods. Specifically, the reviewers raised several points surrounding whether we could exclude ecological variation over years as the explanation of changes with aging, rather than aging itself. Whilst we acknowledge there are limitations to our approach, we provide a comprehensive response to these points highlighting:

(1) Where ecological variables have been accounted for using controls (including the behaviors of other individuals, or an aging individuals' behavior at younger ages).

(2) Where ecological data may be missing, thus a potential limitation to our study, and further data would be beneficial.

(3) Whether, in light of these limitations, interannual ecological variation offers a likely explanation for the behavioral changes we have identified. We provide an argument that whilst ecological data would be desirable for our study, interannual changes in ecology are unlikely to explain the trends in our data. Additionally, we explain why age-related changes, such as senescence, are more likely to underpin the patterns described in our manuscript.

Across 1-3, we have made substantial changes to the reporting of our manuscript to ensure that our results are communicated transparently, and conclusions are made with appropriate care. We have also moved all discussion of coula-nut cracking to the supplementary materials, given the points raised by reviewers about the lack of data describing coula-nut cracking in earlier field seasons.

We hope that these modifications will enhance both the editors' and reviewers' assessment of our manuscript, where we have aimed to make careful conclusions that are supported by our available data. Similarly, we have aimed to communicate the importance of our results across fields of research including primatology, evolutionary anthropology, and comparative gerontology, and hope that our research will be of use to further studies within these subfields.

> ***Reviewer 1 (Recommendations for the authors):***
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> *(1) If possible, include results or a summary of the behaviour of younger adults using stone tools during the same period. It would be helpful to know if they had the same or different pattern to exclude other factors that may influence the tool use (harder nuts in a particular season, diseases, motivation for other foods, etc).*

We include data for other individuals when analyzing attendance. However, we did not collect comparable long-term efficiency data on younger adult individuals for this study. This is, in part, due to the time constraints imposed by long-term behavior coding. Additionally, only one adult was both present at Bossou throughout the 1999-2016 period, and younger than the threshold for our old-age category across these years (thus, the baseline used to compare with older adults would be just one younger adult, thus would not have been useful for characterizing normal variation of many younger adults over time). However, given the longitudinal data we present, we can use data from the earlier field seasons for each elderly focal individual as a personalized baseline control. Previous studies at Bossou find that across the majority of adulthood, efficiency varies between individuals, but is stable within individuals over time (e.g., Berdugo et al. 2024, cited). We detected similar stability in individuals' efficiency over the first three field seasons sampled in our analysis, where there was very little intra-individual variation in tool-using efficiency. However, in later years, two individuals (Velu & Yo) began to exhibit relatively large reductions in efficiency.

These results are unlikely to be explained by ecological variation. If there was a change in ecology underpinning our results, we would expect: [1] changes in ecology to also introduce variation in earlier field seasons, and [2] to influence all individuals in our study similarly. As such, if the changes observed in later field seasons were due to ecological changes, they should have caused a reduced efficiency across individuals, and to a similar degree – we did not observe this result, with large reductions in efficiency were confined to two individuals. Moreover, for Yo (the individual who exhibited the largest reduction in efficiency) we found some additional evidence that changes in oil-palm-nut cracking efficiency extended beyond the period we sampled, i.e. they were evident even in 2018, reflecting a long-term, directional reduction in efficiency as compared to earlier years of her life. This consistent reduction in tool-using efficiency over multiple years adds further weight to the hypothesis that changes at the level of the individual were causing reduced tool-using efficiency, rather than our results being underpinned by interseasonal variation in ecology.

Whilst we agree that our study is limited in the extent to which we can analytically assess ecological explanations for changes in nut-cracking efficiency, we believe that hypothetical ecological changes across field seasons do not predict our results. We now raise both sides of this debate in our discussion, where we outline our limitations (see lines 535-593).

> *(2) The data from 2011 was scarce, with only one individual having 10 encounters. It would be better to be cautious with this season's results.*

We appreciate this limitation raised by the reviewer. Velu and Yo were only encountered a few times in 2011; however, both were encountered more frequently in 2016. For 2011, we did not collect oil-palm nut cracking data for either Yo or Velu. Thus, their change in efficiency was detected by models using data from all other years, regardless of the few encounters in 2011. This sparsity of data may still have influenced our metrics for the proportion of time chimpanzees spent engaging in different behaviors when present at the outdoor laboratory in 2011, particularly for Velu, who was one of the two individuals who exhibited a change in behavior in this year (along with Fana, N = 10 for 2011). We have therefore added a line in our results and discussion highlighting the sparsity of data for Velu when estimating these proportions for 2011 (see lines 255-256 & 410).

> *Minor corrections*
>
> *(1) The last paragraph of the introduction presents many results, which should be in the results section.*

We would like to keep this section of the introduction. Our paper investigates the effect of aging on many different aspects of nut cracking, which could become confusing for readers unless laid out clearly. We believe that having a short summary early on in the paper assists readers with following the methods and arguments presented within our paper.

> *(2) The first section (Sampled data) of the results contains much information that belongs in the methods section.*

We appreciate that there is some overlap between our methods and results section. However as the results section comes before the methods in our manuscript, we wanted to ensure that there is suitable information in our results that allow our results to be interpreted clearly by readers, and that the methods used to generate these results are transparently communicated. For these reasons, we will leave this information in the results, as we believe it increases our paper's readability.

> ***Reviewer 2 (Public review):***
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> *One of the main limitations of this study is the small sample size. There are only 5 of the old-aged individuals, which is not enough to draw any inferences about aging for chimpanzees more generally. Howard-Spink and colleagues also study data from only five of the 17 years of recorded data at Bossou. The selection of this subset of data requires clarification: why were these intervals chosen, why this number of data points, and how do we know that it provides a representative picture of the age-related changes of the full 17 years?*

We note that our sample size is limited to 5 individuals. This is an inevitable constraint of analyzing aging longitudinally in long-lived species, as only few individuals will live to old age. We argue that 17 years is a long enough period of study, as in the initially sampled field season (1999) focal individuals are reaching a mature age of adulthood (39-44 years) and begin to age progressively up to ages that are typically considered to be on the extreme side for chimpanzees' lifespans in the wild (56-61 years). We raise in our methods that whilst it is difficult to determine precisely when chimpanzees become 'old aged', previous studies use the age of around 40 years, as from this age survivorship begins to decrease more rapidly (see Wood et al., Science 2023). Indeed, one focal individual (Tua) disappeared during the period of our study (presumed dead), and one other individual died in 2017 (Velu), the year after our final sampled field season. As of 2025, two other focal females have since died, and only one focal individual was still alive at Bossou (Jire, the individual exhibiting the least evidence for senescence over our study period). These observations suggest that we successfully captured data from chimpanzees during the oldest ages of their lives for most individuals in the community. Moreover, the period of 1999-2016 contains the majority of data available within the Bossou Archive, with years before and after this window containing comparably less data. This information is included within our results and methods (see sections 2.1 and 4.1).

For our earliest field season (1999), it is unlikely that senescence had already had an effect on stone-tool use, as we measured efficiency to be high across all efficiency metrics for all individuals. For example, in 1999, the median number of hammer strikes performed by focal chimpanzees ranged from 2-4 strikes, and this was comparable to the efficiency reported across all adults observed in previous studies at Bossou (Biro et al. 2003, Anim. Cog.). This finding suggests that senescence effects had not yet taken place, allowing us to evaluate whether aging affects efficiency over subsequent field seasons. This point is now included in the manuscript on lines 449-452.

We sampled at 4-to-5-year intervals to balance the time-intensive nature of fine-scale behavior coding against the need to sample data across the extended 17-year time window

available in our study. We limited the final year to 2016 as, in following years, data were collected using different sampling protocols (though, see limited data from 2018 in the supplementary materials). We aimed to keep the intervals between years as consistent as possible (approx. 4 years); however, for some years data were not collected at Bossou, due to disease outbreaks in the region. In these instances, we selected the closest field season where suitable data were available for study (always +/- 1 year). We have provided further clarification surrounding our sampling regime in the methods (see amendments in section 4.1)

> *With measuring and interpreting the 'efficiency' of behaviors, there are in-built assumptions about the goals of the agents and how we can define efficiency. First, it may be that efficiency is not an intentional goal for nut-cracking at all, but rather, e.g., productivity as far as the number of uncrushed kernels (cf. Putt 2015). Second, what is 'efficient' for the human observer might not be efficient for the chimpanzee who is performing the behavior. More instances of tool-switching may be considered inefficient, but it might also be a valid strategy for extracting more from the nuts, etc. Understanding the goals of chimpanzees may be a difficult proposition, but these are uncertainties that must be kept in mind when interpreting and discussing 'decline' or any change in technological behaviors over time.*

We agree that knowing precisely how chimpanzees perceive their own efficiency during tool use is unlikely to be available through observation alone. However, under optimal foraging theory, it is reasonable to assume that animals aim to economize foraging behaviors such that they maximize their rate of energy intake. Moreover, a wealth of studies demonstrate that adult chimpanzees acquire and refine tool-using skill efficiency throughout their lives. For example, during nut cracking, adults often select tools with specific properties that aid efficient nut cracking (Braun et al. 2025, J. Hum. Evol.; Carvalho et al. 2008, J. Hum. Evol.; Sirianni et al. 2015, Anim. Behav.); perform nut cracking using more streamlined combinations of actions than less experienced individuals (Howard-Spink et al. 2024, Peer J; Inoue-Nakamura & Matsuzawa 1997, J. Comp. Psychol.), and as a result end up cracking nuts using fewer hammer strikes, indicating a higher level of skill (Biro et al. 2003, Anim. Cogn.; Boesch et al. 2019, Sci. Rep.). Ultimately, these factors suggest that across adulthood, experienced chimpanzees perform nut cracking with a level of efficiency which exceeds novice individuals, including across the whole behavioral sequence for tool use, even if they are not aware or intending to do so. Previous studies at Bossou have also highlighted that there are stable inter-individual differences in efficiency of individuals over time (Berdugo et al. 2024, Nat. Hum. Behav.). This pattern of findings allows us to ask whether this acquired level of skill is stable across the oldest years of an individual's life, or whether some individuals experience decreased efficiency with age. In addition, our selection of efficiency metrics is in keeping with a wealth of studies which examine the efficiency of stone-tool using in apes, thus, we argue that this is not problematic for our study.

As we stated in our initial responses to reviewers, it is unlikely that tool switching is a valid strategy for tool use, as it is so rarely performed by proficient adult nut crackers (including earlier in life for our focal individuals). Nevertheless, we did not find a significant change in tool switching for oil-palm nut cracking, and this behavioral change was only observed when Yo was cracking coula nuts. As we have now moved discussion of coula nut cracking to the supplementary materials (and tempered discussion of coula nut cracking to emphasize the need for more data) this behavioral variable does not influence our reported results.

In our discussion, we also highlight how seemingly less efficient actions may reflect a valid strategy for nut cracking. E.g. a greater number of tool strikes may reflect a strategy of compensation for progressive tool wear. This would still reflect a reduced efficiency (e.g. in terms of the rate at which kernels can be consumed), but may perhaps borne for the necessity to accommodate for changes in an individuals' physical affordances with aging. Thus, we do

take the Reviewer's point into account, but by using an alternative, more likely, example given the available data. We have now emphasized this point in lines 521-527.

We have also clarified these matters by adding more information into our methods (see lines 798-802 and 828-829), highlighting that we take a perspective on efficiency that reflects the speed of nut processing and kernel consumption, and the number of different behavioral elements required to do so. Our phrasing now explicitly avoids using language that assumes that individuals' have some perception of their own efficiency during tool use.

> *For the study of the physiological impact of senescence of tool use (i.e., on strength and coordination), the study would benefit from the inclusion of variables like grip type and (approximate) stone size (Neufuss et al., 2016). The size and shape of stones for nut-cracking have been shown to influence the efficacy and 'efficiency' of tool use (i.e., the same metrics of 'efficiency' implemented by Howard-Spink et al. in the current study), meaning raw material properties are a potential confound that the authors have not evaluated.*

We did not collect this data as part of our study. Whilst grip type could be a useful variable to measure for future studies, it is not necessary to demonstrate senescence per se. However, we agree that this could be a fruitful avenue to understand changes in behavior at greater granularity, and have added this as a recommendation for further study. We also now provide a discussion on stone dimensions and materials as part of our limitations (see lines 581-589 for both points).

> *Similarly, inter- and intraspecific variation in the properties of nuts being processed is another confound (Falótico et al., 2022; Proffitt et al., 2022;). If oil palm nuts were varying year-to-year, for example, this would theoretically have an effect on the behavioral forms and strategies employed by the chimpanzees, and thus, any metric of efficiency being collected and analyzed. Further, it is perplexing that the authors analyze only one year where the coula nuts were provided at the test site, but these were provided during multiple field seasons. It would be more useful to compare data from a similar number of field seasons with both species if we are to study age-related changes in nut processing over time (one season of coula nut-cracking certainly does not achieve this).*

We have moved all discussion of coula nuts to the supplementary materials so as to avoid any confusion with oil-palm nuts (see comments from Reviewer 2, and our response). Nut hardness may influence the difficulty with which nuts are cracked, with one of the most likely factors influencing nut hardness being its age: young nuts are relatively harder to crack, whereas older nuts, which are often worm-eaten or can be empty, crack more easily, yet are not worth cracking (Sakura & Matsuzawa, 1991; Ethology). We largely controlled for this in our study, as the nuts provided at outdoor laboratories were inspected to ensure that the majority of them were of suitable maturity for cracking, and we now clarify this control in our methods (see lines 678-680) and when discussing our study limitations (see lines 551-558). In these sections, we also highlight a previous study at Bossou that shows chimpanzees select nuts which can be readily cracked, based on their age (Sakura & Matsuzawa, 1991; Ethology).

We acknowledge that we are limited in the extent to which we can control for interannual variation in ecology with our available data. However, we highlight why interannual variability is unlikely to fully explain our results (see lines 551-580 and response to comments from Reviewer 1). We also highlight in our limitations section that future studies should (where possible) aim to collect more ecological data to account for possible confounds more rigorously.

> *Both individual personality (especially neophilia versus neophobia; e.g., Forss & Willems, 2022) and motivation factors (Tennie & Call, 2023) are further confounds that can contribute to a more valid interpretation of the patterns found. To draw any conclusions about age-related changes in diet and food preferences, we would need to have data on the overall food intake/preferences of the individuals and the food availability in the home range. The authors refer briefly to this limitation, but the implications for the interpretation of the data are not sufficiently underlined (e.g., for the relevance of age-related decline in stone tool-use ability for individual survival).*

In our discussion, we highlight that multiple aging factors may influence apes' dietary preferences and motivations to attend experimental (and perhaps also naturally-occurring) nut cracking sites (see lines 397-443 and 542-550). We do not believe that neophobia is a likely driver underlying our results, given that the outdoor laboratory has been used to collect data for many decades, including over a decade prior to the first field season in which data were sampled for our study (now highlighted in lines 692-694). In addition, previous studies at Bossou have determined that the outdoor laboratory is visited with comparable frequency to naturallyoccurring nut cracking sites, which makes any form of novelty bias unlikely (this information is now included in our methods, see lines 397-400, and also 687-689).

We agree that further information is required about foraging behaviours across the home range to understand changes in attendance at the outdoor laboratory, and have now provided more clarity on this within the limitations section of our discussion 542-550. In our discussion of individual survivability, we state clearly that we cannot make a conclusion about how changes in tool use influence survival with the available data, and assert that this would require data across the home range (see lines 627-638). We agree that future research is needed to assess whether changes in tool use would influence survivability, and also suggest that it may not be survival-relevant; instead changes in tool use with aging may simply be a litmus test for detecting more generalized senescence.

> *Generally speaking, there is a lack of consideration for temporal variation in ecological factors. As a control for these, Howard-Spink and colleagues have examined behavioral data for younger individuals from Bossou in the same years, to ostensibly show that patterns in older adults are different from patterns in younger adults, which is fair given the available data. Nonetheless, they seem to focus mostly on the start and end points and not patterns that occur in between. For example, there is a curious drop in attendance rate for all individuals in the 2008 season, the implications of which are not discussed by the authors.*

As the reviewer points out, when examining the attendance rates of older individuals over sampled field seasons, we used the attendance rates of younger individuals as a control. However, we do not run this analysis using start and end points only. Attendance rates were included in our model across the full range of sample field seasons. However, as the key result here is an interaction term between age cohort (old) and the field season (scaled about the mean), we supplement this significant statistical result with a digestible comparison of attendance rates between the first and last field season, to give a general sense of effect size. We have clarified that all data were used in our model (see line 229, and also the legend for Table 2), and in this section we also provide all key model outputs and signpost where the full model output can be found in the supplementary materials.

> *As far as attendance, Howard-Spink and colleagues also discuss how this might be explained by changes in social standing in later life (i.e., chimpanzees move to the fringes of the social network and become less likely to visit gathering sites). This is not senescence in the sense of physiological and cognitive decline with older age. Instead, the*

> *reduced attendance due to changes in social standing seems rather to exacerbate signs of aging rather than be an indicator of it itself. The authors also mention a flu-like epidemic that caused the death of 5 individuals; the subsequent population decline and related changes in demography also warrant more discussion and characterization in the manuscript.*

We have adapted this part of the discussion to make it clear that social aging is not necessarily equivalent to physiological and cognitive aging. We have also clarified in this section the changes in demography at Bossou during our study, which may have further impacted social behaviors (see lines 423-443).

> *Understandably, some of these issues cannot be evaluated or corrected with the presented dataset. Nonetheless, these undermine how certain and/or deterministic their conclusions can really be considered. Howard-Spink et al. have not strongly 'demonstrated' the validity of relationships between the variables of the study. If anything, their cursory observations provide us with methods to apply and hypotheses to test in future studies. It is likely that with higher-resolution datasets, the individual variability in age-related decline in tool-use abilities will be replicated. For now, this can be considered a starting point, which will hopefully inspire future attempts to research these questions.*

We thank the reviewer for their comments. We have adapted our manuscript to highlight that we agree that it serves a starting point for answering these valuable questions; however, we do feel that we can contribute meaningful evidence that it is likely aging effects underlying the findings in our data (see responses above). We agree with the reviewer that further study is needed to understand these questions in more detail, and have tried to ensure that our conclusions are suitably tempered, and the recommendations for research are heavily encouraged to build on our findings.

> *Falótico, T., Valença, T., Verderane, M. & Fogaça, M. D. Stone tools differences across three capuchin monkey populations: food's physical properties, ecology, and culture. Sci. Rep. 12, 14365 (2022).*

This has now been cited.

> *Forss, S. & Willems, E. The curious case of great ape curiosity and how it is shaped by sociality. Ethology 128, 552-563 (2022).*

We do not cite this – see above.

> *Neufuss, J., Humle, T., Cremaschi, A. & Kivell, T. L. Nut-cracking behaviour in wild-born, rehabilitated bonobos (Pan paniscus): a comprehensive study of hand-preference, hand grips and efficiency. Am. J. Primatol. 79, e22589 (2016).*

This has now been cited.

> *Proffitt, T., Reeves, J. S., Pacome, S. S. & Luncz, L. V. Identifying functional and regional differences in chimpanzee stone tool technology. R. Soc. Open Sci. 9, 220826 (2022).*

This has now been cited.

> *Putt, S. S. The origins of stone tool reduction and the transition to knapping: An experimental approach. J. Archaeol. Sci.: Rep. 2, 51-60 (2015).*

We do not cite this, as we instead cite studies which highlight chimpanzees' ability to become more efficient in tool use with repeated practice (see above).

> *Tennie, C. & Call, J. Unmotivated subjects cannot provide interpretable data and tasks with sensitive learning periods require appropriately aged subjects: A Commentary on Koops et al. (2022) "Field experiments find no evidence that chimpanzee nut cracking can be independently innovated". ABC 10, 89-94 (2023).*

We do not cite this – see above

> ***Reviewer #2 (Recommendations for the authors):***
>
> *Minor Comments:*
>
> *(1) Line 494: Citation #53 is listed twice.*

This has been amended.

> *(2) Line 501: The term 'culturally-dependent' as used here is, at best, controversial, and at worst, misapplied. I would recommend replacing it with simply the term 'cultural'.*

This has been changed to 'cultural'.

> *Major Comments:*
>
> *For the Introduction, in the paragraph starting on Line 91, and the Discussion, starting on Line 369, I would recommend some simple re-structuring of the argumentation. As many in the Public Review, the changes in social standing according to age are not necessarily a case of senescence in the very sense of physiological or cognitive changes of the individual. This seems to have had an effect on attendance rates, which then could have been a driver of behavioral changes and even cognitive decline as ostensibly measured by the other variables. The social impact of aging should be mentioned in the Introduction (it is not currently) and the social and physiological/cognitive effects of aging should be separated in the Discussion. You can then discuss more clearly how the former via other behavioral changes can accelerate the latter (or not).*

We take the point raised about social aging. Integrating information about social aging into the introduction was challenging without disrupting the flow of the paper; however, we have included these valuable points in the discussion (see lines 423-443). We now structure this section to clearly distinguish social aging, and discuss how, in tandem with changes in demography at Bossou, it may have influenced rates of attendance to the outdoor laboratory over the years. We do not go into detail about how social aging may interact with physiological or cognitive effects of aging, as we cannot support this with the available data, however we highlight at the end of this paragraph how all of these possible factors require further investigation.

> *For the present study, it will either be impossible or impractical to gather data on the yearly ecological conditions, contextualized dietary preferences, individual personalities, etc., so I would not ask that you do so. It is important, however, to temper some of the claims being made in the manuscript about what you have 'determined' about the nature of senescence in chimpanzees and to be more transparent about the limitations and potential confounds when interpreting the data. To avoid repetition, the key points can be found in the Public Review under 'Weaknesses'.*

We appreciate the reviewer's understanding of the limitations of our study. Some of these factors – such as individual personalities and dietary preferences – are addressed somewhat by our use of long-term data at the level of the individual, particularly in the analyses of efficiency, where we model individuals' behaviors compared to those in earlier years offers an individuallybespoke control. However, there are other ecological variables of possible importance that we cannot evaluate. We now address several of these points raised by reviewers in the discussion, to ensure transparency of reporting (see limitations section of our discussion, and results to the comments provided by Reviewer 1, and our responses to points raised in the Public Review). We have also tempered some of the phrasing surrounding our conclusions, where we say that this is the first evidence that aging can impact chimpanzee tool use, we also highlight the need for an assortment of further studies.

> *Finally, the integration of the coula nut-cracking data is not well-executed as it stands. I would recommend that they collect and analyze equivalent behavioral data from the other years where coula nuts were provided. By examining only one season of coula nut-cracking, we cannot contextualize the data to past seasons; there is no sense in comparing one season of coula nut-cracking (i.e., in a sense of efficiency) to roughly contemporary seasons of palm-nut cracking due to, as you describe, differences in physical properties of the nuts. If you are not able to collect the additional data and carry out the requisite analysis, then I would recommend that the coula nut-related sections be removed from the manuscript, so that it does not detract from the logical flow of arguments and distract from the other data, which is more logically-attuned to your research questions.*

We have removed this from the main manuscript. We have decided to include the information surrounding coula nut cracking in the supplementary materials, as this information is still relevant to the findings of our study, and may interest some readers. However, we have phrased this information to make it clear that further data is needed to compare coula nut cracking across years.

> *These criticisms do not subtract from the (potential) value or importance of the work for the field. This is, of course, an important contribution to an understudied topic. As such, I would gladly advocate for the manuscript, assuming the authors would reflect on the listed caveats and make changes in response to the 'Major Comments'.*

We thank the reviewer for their comments.

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