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the reserve, and regular monitoring of animals and human activity is important and necessary. Ideally, the local communities will take the initiative in carrying out regular monitoring and patrolling of their forests. Our ICBR project is a model case of collaboration among local communities, conservation NGOs and scientific researchers. At this stage of the ICBR project, the collaboration is expected to continue to help solve current problems and facilitate development of the management plan.

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<NOTE>

Death of the Oldest Female at Mahale and Some Notes about Longevity of Wild Chimpanzees

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DEATH OF CALLIOPE, THE OLDEST FEMALE AT MAHALE

Calliope (Figure 1), an old, female chimpanzee at Mahale, is assumed to have died this past year (*i.e.*, 2012). Her death is *assumed* because it has not been confirmed, but she has not been witnessed since the final observation

on 5th April 2012. As it is rare to observe the deaths of wild chimpanzees directly, or to find the dead bodies, we usually assume individuals who have not been observed for more than 3 consecutive months in Mahale to be deceased.

Calliope was estimated to be 52 years old in 2012, which is the oldest age at death so far recorded at Mahale. She was first identified in 1973 as a young adult. The starting age of adulthood in females is 13 years old. Therefore, she would have been at least 13 years old at that time. This gave the estimation that she was born in 1960, but her exact birth-year could be even earlier.

According to Nishida¹, Calliope had been very shy to human observers until the 1990s. Although she later became tolerant of observations from a certain distance, she continued to be more timid than the other females. She seemed reluctant to get too close to humans, especially when she had a small baby. Throughout her life, Calliope gave birth to a minimum of 5 offspring (*i.e.*, 3 females and 2 males)². Except for 1 female offspring who died at 3 years old, the other 4 were weaned and reached the age of puberty. Thus, it can be said that she was a successful mother. After she gave birth to her last offspring in 1997, she did not give birth again throughout the last 15 years of her life. Excluding the 5 years during which she was nursing her last baby, she enjoyed her remaining post-reproductive life for 10 years.



Figure 1. Calliope in 2010 (at estimated age of 50 years old). Although her hair was white, she did not look old.

CALLIOPE'S FINAL DAYS OF LIFE

Calliope was often observed traveling with her last daughter, Carmen, until Carmen emigrated from the M group in July 2011. Calliope also groomed often with her two mature sons, Carter and Cadmus, when she met them. After the emigration of Carmen, Calliope often

ranged together with Wakusi, an older female who is estimated to be one year younger than Calliope. As the oldest duet, they usually kept a moderate distance from noisy males, even though they both had mature sons. However, in large, they ranged alongside the other chimpanzees. We sometimes observed that they would feed apart from the others, whose calls could be heard from a distance. Some moments later, they would travel in the direction of the calls in tandem. When they caught up with a group of males, the males would often groom the two older females. The females, however, seldom groomed the males in return, as if they were enjoying respects for the aged. Calliope might have suffered from presbyopia. For instance, when she groomed others, she straightened up her upper body so that her eyes were at a distance from the groomee's body surface.

When MN observed Calliope on 15th December 2011, she was, again, travelling with Wakusi. When these two, and a mother-infant pair, were resting under a bush, there came her fully adult son, Carter. Then, Calliope and Carter started to play with each other. They tickled, slapped, and mouthed each other's body and chased each other in a circle. Both of them showed a play face and play panted. A 51-year-old mother and a 26-year-old adult son were playing like two juveniles! The play lasted for 23 minutes.

HN was the last researcher to see Calliope on 4th March 2012, when he was following an adult male who was in consort with a young estrous female. On this day, again, Calliope and Wakusi were together. The two joined the party that HN was following. Although the observation time for Calliope was short, HN did not notice anything peculiar about her health or physical condition. After that day, she was not observed again for some time. This is not uncommon in March–April, however, as Mahale chimpanzees are usually dispersed in small parties throughout this season. On 5th April 2012, a research assistant observed Calliope with 10 other chimpanzees. This was the last day that she was observed.

LONGEVITY OF WILD CHIMPANZEES

Establishing the longevity, or the maximum lifespan, of wild chimpanzees is difficult to ascertain. Chimpanzees typically have a long lifespan, and their ages are often estimated. Let us compare, here, the 52 years of life of Calliope (the longest documented lifespan at Mahale) with other wild chimpanzee populations. At Gombe, the oldest estimated age at death was 53 years for the famous chimpanzee, Flo³. At Bossou, the oldest female, Kai, died at an estimated 53 years of age⁴. At Tai, a female, Chanel, died when she was 46 years old (calculated from Appendix Table A.1. in ref. 5). These ages are all within the estimated range of the maximal lifespan potential of captive chimpanzees (48 ± 5 years; taken from a literature survey covering over 100 zoos worldwide; cited in ref. 6).

We have to be careful about the specific age at death for chimpanzee individuals in the wild because they are all estimates. For example, Flo's age at death was first estimated to be 43 years old by Goodall⁷, but she was estimated to be 10 years older in the later literature³. This

may be because Flo was already old, in her 30s or 40s, when she was first identified in 1962. Estimating the age of older individuals is particularly difficult because individuals differ in their appearance. Like humans, some chimpanzees look younger and others look older than they really are. Accordingly, we see, with a bit of suspect, that a 55-year-old mother gave birth to a child at Kibale⁸. This means that, if the estimation of age is correct, her longevity will be much longer than that of previously recorded individuals. Research at Kibale was initiated in 1983⁹, which means this female was in her 30s at that time. Thus, there may be the possibility that her age was overestimated.

For the estimated age of Calliope, we expect a small proportion of error because she was estimated to be 13 years old when she was first identified. It is possible that one would estimate a 33-year-old female to be 43 years old, but it is not likely that one estimates a 3-year-old female to be 13 years old. From our experience, estimation error of a 13-year-old female can be within 3 years or so, thus we can more confidently say that Calliope was between 49 and 55 years old at the time of her death.

Finally, we should mention some aged individuals who are still alive. At the time of writing, there were several older chimpanzees at Mahale, such as Wakusi (female, 51), Gwekulo (female, 50), Fatuma (female, 49) and Kalunde (male, 49) (numbers in parentheses are their estimated ages in 2012, which are equally accurate as, or even more accurate than, that of Calliope because these individuals were in their young adulthood or adolescence when identified). Some of these individuals now look old in their appearance and show the typical behavioral characteristics of old age, such as slow traveling speed and a relative decrease in activity. However, at present, they all appear to be in good health. Similarly, at Bossou, 4 females and 1 male older than 50 years were still alive in 2012 (Ohashi G, personal communication). Looking at these figures, although the sample size is still small, it seems that more females experience old age than males at both sites. This assumption concurs with the fact that males, on average, show higher mortality than females¹⁰.

We hope that these older chimpanzees will live longer, well beyond the current records of longevity in wild chimpanzees. Then, our current knowledge about the longevity of wild chimpanzees would be revised.

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sumed in broader studies of manual behaviour, e.g. ref. 5. Furthermore, studies often do not distinguish between aimed (targeted) throwing *versus* unaimed (perhaps better termed hurling) throwing, underarm *versus* overarm delivery, or one-handed *versus* two-handed throwing.

Several studies of manual laterality in throwing by captive chimpanzees have been published, and all have reported population-level, right-sided bias^{6–8}. Others have incorporated these reported findings into comprehensive accounts of the origin of handedness, e.g. ref. 9

We can find no published quantitative data on manual laterality in throwing from *any* non-human primate species in nature, much less from chimpanzees. One obvious reason for this absence is that, unlike in the artificial conditions of captivity, wild primates throw only rarely. Here we report such a dataset, collected ethologically from a population of chimpanzees in nature, over an extended period, in an effort to balance the picture.

METHODS

The subjects were the eastern chimpanzees (*Pan troglodytes schweinfurthii*) of M group in the Mahale Mountains of western Tanzania^{10,11}. This population has been studied since 1965, making it the second-oldest field study of chimpanzees; the apes are fully habituated to close-range behavioural observation. The Mahale ethogram is well-known and described; Nishida *et al.*¹² listed 10 kinds of throwing.

We recorded all observed occurrences of throwing, using *ad lib.* sampling, that is, regardless of whether behaviour was being scan-sampled or focal-subject-sampled¹³. We interrupted normal protocols, in order to note the identity of the thrower, target, etc. Nishida recorded his data from 1999–2004, when he mostly followed males, hence the shortage of data on females. McGrew and Marchant recorded their data in 1996. Here we report data only on unimanual *versus* bimanual data, and on the hand(s) involved. Each throw is considered an independent data-point, as the chimpanzees always repositioned themselves between throws, usually to pick up another object.

RESULTS

We recorded 556 throws by 16 individuals (Table 1); the median number of throws per subject was 33 (range: 9–72). Of these, 63 (11%) were done two-handed, usually in agonistic charging displays; almost half of these were done by two high-ranking adult males (DE, $n = 17$; FN, $n = 13$). These appeared to be unaimed and perforce were done bipedally; they are considered no further here.

One-handed throwing was unlateralized. Only 4 (BB, CT, IV, OR) of the 16 individuals showed statistically significant (Binomial test, two-tailed, $p < 0.05$) laterality; three were biased to the right versus one to the left. The remaining 12 subjects showed ambilateral performance. Overall, nine individuals showed (non-significantly) more right-sided throws, six showed left-sided throws (a non-significant difference, $n = 15$, $x = 6$, $p = 0.60$), and one was tied. Descriptively overall, of one-handed throws, 226 (46%) were done with the left hand versus 267 (54%) with the right hand.

<NOTE>

Wild Chimpanzees at Mahale are not Manually Lateralised for Throwing

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INTRODUCTION

The importance of throwing has figured consistently and prominently in scenarios about the evolutionary origins of human behaviour^{1,2}. The utility of imparting force to airborne projectile weapons, launched ballistically, is obvious, whether to deter, punish or subdue predators, prey, or competitors. Other functions of throwing are less obvious but could be equally useful, such as bringing down hanging fruit, gaining others' attention, shattering large objects into fragments, etc. Scenarios have stressed a number of important variables, such as posture (especially bipedality), sensorimotor skill (especially hand-eye coordination), cerebral asymmetry, etc. Calvin¹ linked all of these to the evolutionary origins of language. However, few of these ideas have been tested empirically.

One way to tackle evolutionary aspects of human throwing is to look at throwing performance in our nearest living relations. Although throwing has been known in both wild³ and captive⁴ chimpanzees for almost a century, quantitative studies are few; often they are sub-