Longevity in gibbons (*Hylobatidae*)

Thomas Geissmann[1], Katja Geschke[2] and Barbara J. Blanchard[2]

[1] Anthropological Institute, University Zürich-Irchel,
Winterthurerstr. 190, CH–8057 Zürich, Switzerland
E-mail: thomas.geissmann@aim.uzh.ch

[2] Wellington Zoo Trust, 200 Daniell Street,
Newtown, Wellington 6021, New Zealand

A longevity record of 60 years spent in captivity by a Mueller's gibbon (*Hylobates muelleri*) is reported here. This appears to be the second-highest age so far reported for a non-human primate, but it is especially remarkable when adjusted for body size. It is well known that longevity in mammals correlates with body weight. Small apes should, therefore, be expected to exhibit lower longevity than the great apes because of their lower body weight. However, the longevity record for *Hylobates* reverses this expectation for great apes like orangutans (*Pongo*) and gorillas (*Gorilla*). This study further found a significant correlation between the captive population size of primate genera and their recorded longevity. A comparison of longevity and captive population size suggests that recorded longevity in the gibbon genera *Hoolock*, *Nomascus* and *Symphalangus* is lower than that of the genus *Hylobates* because *Hylobates* is kept in captivity in much higher numbers. As a result, data on *Hylobates* longevity are obtained from larger sample sizes than that of all other gibbons. This suggests that all gibbon genera may eventually be revealed to exhibit an elevated longevity in relation to their body weight when larger amounts of data become available. Longevity data for great apes, in contrast, are based on larger samples than those for most genera of the small apes, and an increase in sample size for great ape genera may less likely produce a substantial increase in the longevity record.

Introduction

Longevity is an essential variable for research on the biology of ageing (Sacher, 1975). It may also be of practical use to zoos and other breeding facilities in order to assess the breeding potential of animals of known age. Longevity of captive mammals in general, and primates in particular, has repeatedly been tabulated (Carey and Judge, 2000; Flower, 1931; Jones 1962, 1968, 1979, 1982; Weigl, 2005).

Longevity is closely related to several other constitutional dimensions, including body weight, brain weight, metabolic rate, and body temperature, which account for about 70% of the lifespan variance in mammals (Sacher, 1975). Longevity also correlates with the size of various other body organs (Austad and Fischer, 1992). Some taxonomic groups are particularly long-lived. Primates, for instance, are long-lived mammals, the great apes have been identified as long-lived primates, and humans are long-lived apes (Carey and Judge, 2000). Gibbons, however, have not been identified previously as particularly long-lived primates, and even less as long-lived hominoids. Our case study on a Mueller's gibbon (*Hylobates muelleri*) kept at the Wellington Zoo, suggests that exactly this may be the case.

We provide detailed documentation that is as complete as possible on the past life of our study animal, a male Mueller's gibbon, with the aim of verifying his unusually high age. This is necessary, as various reports on unusual longevity in apes are not supported by convincing evidence (Puschmann and Federer, 2008). The most illustrious among these apes is "Cheeta", the chimpanzee (*Pan troglodytes*) who was awarded a certificate for being "the world's oldest living primate, aged 69 years and one month" by the Guinness Book of World Records in 2001. The chimpanzee was allegedly brought in 1932 as a young animal from Liberia to the U.S.A. and co-starred as Cheeta with Johnny Weissmuller in MGM's Tarzan movies of the 1930s and '40s. According to numerous newspaper and internet reports, "Cheeta" has been reported to have reached 76 years of age in 2008 (e.g. Adams, 2008; Martinez, 2008; Nash, 2008; Neate, 2008; Wikipedia contributors, 2008), although this age cannot be supported by concise information. This long life span differs considerably from the values reported in primate longevity studies (59 years 5 months, e.g. Weigl, 2005). The high age of Cheeta is unlikely for several reasons: Various chimpanzees with the same official name were trained together for the same film roles. None of the film chimpanzees exhibited facial features that could linked with the current Cheeta. The published age of Cheeta has repeatedly gone up and down in subsequent reports. Based on the ape's external features, his birth date was more likely to have been in the 1960's than in the 1930's (Rosen, 2009; Puschmann and Federer, 2008; Weigl, 2009; Weigl, personal communication to TG, Aug. 2008).

This article is part of a series of papers reassessing vital statistics of gibbons, such the age of sexual maturation and gestation length (Geissmann, 1991), neonatal body weight (Geissmann and Orgeldinger, 1995), and adult body weight (Geissmann, 1998, in prep.), and ovarian cycle duration (Geissmann and Anzenberger, 2009).

Methods

Longevity data used in this study were extracted from Weigl (2005). Only for two primate species were other sources used because their longevity values were considerably higher than those reported by Weigl (2005). These species include *Hylobates muelleri* (this study, see Results), and the chimpanzee (*Pan troglodytes*). The oldest chimpanzee is believed to be 76 years old (Adams, 2008; Martinez, 2008).

For each genus, the species with the longest known longevity was determined. The body weight of that species was extracted from Gordon (2006). The body weights used in this study are from adult, wild-caught primates, and are an average of mean male body weight and mean female body weight.

Several primate genera were excluded from the study because their longevity data were considered unrealistically low. Low longevity estimates usually occur in taxa that are rarely kept in captivity. The excluded primate genera are: *Avahi*, *Indri*, *Hapalemur*, *Prolemur*, *Lepilemur*, *Euoticus*, *Arctocebus*, *Brachyteles*, *Oreonax*, *Piliocolobus*, *Procolobus*, *Nasalis*, and *Presbytis*. The genus *Homo* was also excluded because its current longevity is not believed to be comparable to that of non-human primates. Additional genera were also excluded because no reliable body weight data appear to be available for the species with the highest longevity (Gordon, 2006). These genera are *Allocebus*, *Callimico*, *Cacajao*, *Callicebus*, *Allenopithecus*, *Lophocebus*, and *Pygathrix*. A total of 48 genera were included in the analysis.

We also wanted to test whether longevity data were influenced by the sample size of individuals used to determine longevity. Although the captive population size of each genus was unknown, numeric proportions among the genera can be estimated by using the numbers of animals of each genus currently living in ISIS (International Species Information System) member institutions (ISIS, 2008). These institutions include 735 zoos and aquariums in 73 countries. The captive population size of each genus was extracted from the ISIS website on 23 July 2008.

Statistical calculations were carried out using JMP v. 7.0 software.

Three tape-recordings of the study animal "Nippy" at Wellington Zoo were available for this study: (1) Recording on audio cassette, unknown recordist, carried out c.1974, made available by Graeme Strachan. Recording duration 1'08", short section of a song bout. (2) Recording on audio cassette, by Graeme Strachan, carried out in August 2001. Recording duration 31'36", virtually complete song bout. (3) Recording on microcassette carried out by one of us (BJB) on 4 Aug. 2008 at about 12:00 hrs, using a SONY recorder M-607V. Recording duration 1'32", short fragments of a song bout of about 30 minutes duration.

Sonagrams of fully developed male song phrases were generated and measured by one of us (TG) using Raven 1.3 software (Cornell Laboratory of Ornithology, Ithaca, NY, U.S.A.) on a Macintosh PowerBook G4. The following spectrogram parameters were selected: Hann window, size = 39.8 ms = 1756 samples, 3 dB bandwidth = 36.1 Hz, time grid overlap = 75%, grid size = 9.95 ms, DFT (Discrete Fourier Transformation) size = 4096 samples (Charif *et al.*, 2007).

Results

Nippy: A biographical summary

Nippy arrived at Wellington Zoo on 2 Dec. 1949 as an 18" (46 cm) high youngster, together with a mate (Anonymous, 1949a). They arrived on the freighter Wairata coming "from Rangoon, Calcutta, Singapore, Java, and Sourabaya, via Auckland, with a variety of animals for the Wellington zoo".

The gibbons' exact origin is unknown, because the zoo's records were water damaged after a fire in the 1970's (Hill, 1999). According to one source, the two gibbons were rumoured to have been obtained from the Sultan of Johore (Anonymous, 2008). According to another they were bought from "the director of the Singapore Zoo" for £ 180 (Anonymous, 1950), but the Singapore Zoo has been in existence since only 1973. Probably there was a zoo in Singapore before that and the director acquired animals locally for overseas orders, so there could be some truth in both stories, though we can't derive any conclusions.

Upon arrival, the young pair of gibbons was described as "two agile long-armed gibbons" (Anonymous, 1949b), and Nippy was described later as a gibbon with a "solemn black face and grey fur" (Anonymous, 1954a).

Apparently, Nippy was originally identified as an agile gibbon (*Hylobates agilis*). His origin was suggested to be Borneo (Anonymous, 1950, 1953, 1954b, 1999) or Assam (Anonymous, 1954a). In 1995, his identification was changed to white-bearded gibbon (*H. albibarbis*) (G. Strachan, cited in Anonymous, 2008). In 2001, Nippy was identified by one of us (TG) as a Müller's gibbon (*H. muelleri*, probably *H. muelleri abbotti*) from Borneo, based on tape-recordings of his calls and photographs provided by Graeme Strachan. In 2004, this identification was confirmed and specified as Grey Müller's gibbon (*H. muelleri abbotti*) from northwestern Borneo, based on a new set of photographs.

Nippy's old accession number at Wellington Zoo was 0051; he was re-entered as M10 on 14 July 1981.

Nippy featured in the news and other media repeatedly (Anonymous 1949a, b, 1950, 1953, 1954a, b, 1987, 1997, 1999, 2004; 2005; Henderson, 2002; Hill, 1999; NZPA, 2004; Strachan, 2001; Wellington City Council, 2004). The earliest photograph of one of the two gibbons available to us was published in a newspaper of 1950 (Anonymous, 1950), but the quality of the preserved copy does not allow to recognize much more than the gibbon's shape. Two better newspaper photos were published in 1954 (Anonymous, 1954a, b), when Nippy was about 6 years old (Fig. 1). Two photographs from later press reports are shown in Figs. 2 and 3.

Fig. 1. Gibbon male Nippy, c.1954, at an estimated age of 6 years. Photo: unknown, previously published in Anonymous (1954b). – *Das Gibbon-Männchen Nippy um 1954, im geschätzten Alter von 6 Jahren*.

Fig. 2. Gibbon male Nippy in 1961, at an estimated age of 13 years. Photo: Rod Blanchard. – *Das Gibbon-Männchen Nippy im Jahr 1961, im geschätzten Alter von 13 Jahren*.

Fig. 3. Gibbon male Nippy, c.1987, at an estimated age of 39 years. Photo: unknown, previously published in Anonymous (1987). – *Das Gibbon-Männchen Nippy um 1987, im geschätzten Alter von 39 Jahren*.

A newspaper article from December 1953 reported that Nippy had recently fallen from a perch, breaking three ribs and other bones, but was fully recovered at the time of the report (Anonymous, 1953).

Nippy's first mate died about a year after arrival (Hill, 1999). Although the date of her death is unknown, it is known that the male was residing in solitary state at least since 1954 and possibly earlier (Anonymous, 1954a).

Around the year 1970, a new partner for Nippy arrived from Winnipeg Zoo (Canada). This female was reportedly a capped gibbon (*H. pileatus*) and was diagnosed as epileptic on 4 March 1970. She gave birth prematurely to a still-born offspring on 15 Nov. 1972, and was found dead on 31 March 1979.

Around January 1981, a female spider monkey ("Goldie", M24) – identified in the zoo records as a Geoffroy's spider monkey (*Ateles geoffroyi*) – was put together with Nippy to give each other company, and they lived together amicably.

Nippy was originally kept in a cage of the "old gibbon block", until he was moved to the former chimpanzee cage around 1981. After that cage was condemned around 1982, Nippy and Goldie were taken off display. They were housed in the quarantine unit around 1990. As they didn't seem to be happy there, they were moved to the hospital soon after where they got frequent visits from staff, friends and visiting groups, though off-limits for the normal zoo visitor. The indoor cage (area 2.21 x 2.8 m) had fiberglass insulation and a black heater, set no lower than 20°C. The outdoor part (area 4.5 x 9.3 m, height 2.5 m) had "porch" areas and was divisible into two, but usually Nippy and Goldie had access to both parts, unless the cage was needed for another inmate of the hospital.

The spider monkey Goldie died on 16 Oct. 1996 from an infection. After that, Nippy was kept solitary.

Nippy had various health problems over the years, and some of them were probably related to his progressing age. These are described in one of the following sections.

Nippy was euthanised on 2 Sep. 2008. He had been found in the morning of the same day unable to move and with clinical signs of a stroke. The autopsy revealed signs of a geriatric animal with general muscle atrophy and worn teeth. His organs showed signs of degenerative lesions in the liver, kidney and heart. The histopathology results of the brain were not conclusive.

Nippy's death was commented upon in numerous internet and newspaper reports (e.g. Anonymous, 2008b, c, d, e, f, g, h; Ikram, 2008; Ling, 2008; Nagpal, 2008).

Nippy's age at death

Previously published reports differ as to how old Nippy was on arrival, ranging from 1 year (Anonymous, 2008b, f; Ling, 2008), 1.5 years (Anonymous, 1997), 2 years (Henderson, 2002), to 2-3 years (Strachan, 2001). For many years, the gibbons were cared for by Mr Frank Coles who knew Nippy since 1949 (Anonymous 2004, NZPA, 2004). He remembers that Nippy did not need bottle feeding when he arrived and estimates the gibbon's age at arrival to have been just over a year old (F. Coles, personal communication to BJB, 23 April 2009). Nippy's height measurement at arrival (46 cm, Anonymous, 1949a) seems to confirm this estimate, if the measurement refers to standing height and not sitting height. In a study on the development of captive agile gibbons (*H. agilis*), an individual of 1.23 years of age had a standing height (determined by combining sitting height and leg length) of 47.5 cm (Suzuki *et al.*, 2003). As this height is nearly identical to Nippy's, 1.2 years may be a reasonable estimate for Nippy's age at arrival.

Nippy lived in Wellington from 2 Dec. 1949 to 2 Sep. 2008. This is a time span of 58 years and 10 months or 58.83 years. If Nippy was 1.2 years old at arrival, he was 60 years old when he died.

Health problems and age-related changes

Already in 1987, Nippy was described as the "old man of the zoo" (Anonymous, 1987).

In June 1991, Nippy's upper canines were removed. He had worn incisors and a missing lower incisor before his upper canine teeth were extracted. Ever since the upper canines were removed, he had opaque mucoid discharge from eyes and nostrils sporadically, probably due to a chronic infection in the lacrymal gland. As a result, Nippy's nose and eyes were often congested and with crusting around eyes (see photographs in Figs. 4 – 11). As treatment under anesthesia was considered risky due to Nippy's age, and as his nasal/ocular congestion/discharge did not appear to affect him adversely, he was permanently treated with antibiotics for this condition. Goldie, the spider monkey, cleaned up Nippy's face regularly, and in return he teased her regularly by touching her as he swung past, or pulling her tail a little. Basically they got on very well.

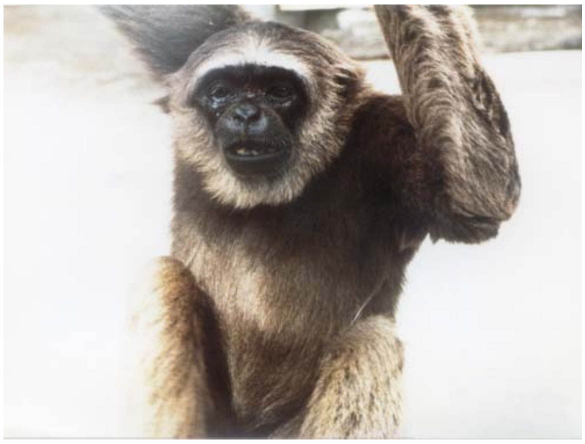

Fig. 4. Gibbon male Nippy on 26 Mar. 1996, at an estimated age of 48 years. Photo: Richard Weigl. – *Das Gibbon-Männchen Nippy am 26. März 1996, im geschätzten Alter von 48 Jahren*.

Fig. 5. Gibbon male Nippy on or near 2 Dec. 1998, at an estimated age of 50 years. Photo: unknown photographer, probably from Wellington City Council. – *Das Gibbon-Männchen Nippy im Dezember 1998, im geschätzten Alter von 50 Jahren*.

Fig. 6. Gibbon male Nippy yawning, c.1999, at an estimated age of 51 years. Notice worn dentition and loss of several teeth (including lower incisors). Photo: courtesy of Wellington City Archives, previously published in Anonymous (1999). – *Das Gibbon-Männchen Nippy um 1999, im geschätzten Alter von 51 Jahren. Die Bezahnung ist stark abgenutzt und mehrere Zähne fehlen, darunter die unteren Schneidezähne*.

Fig. 7. Gibbon male Nippy on 23 Nov. 1999, at an estimated age of 51 years. Photo: Neil Price. – *Das Gibbon-Männchen Nippy am 23 November 1999, im geschätzten Alter von 51 Jahren*.

Although Henderson (2002) suggested that Nippy's "fur may be getting greyer" as a result of his old age, it is unknown whether this is a speculation by the newspaper reporter or based on actual observations by his informants. The colour photos we were able to examine do not provide reliable evidence to prove or disprove that an age-related change in Nippy's fur colouration occurred. None of these colour photographs predate 1996, however.

Fig. 8. Gibbon male Nippy at foraging tray on 14 Oct. 2002, at an estimated age of 54 years. Photo: Pauline Wirihana. – *Das Gibbon-Männchen Nippy an seiner Futterkiste am 14 Okt. 2002, im geschätzten Alter von 54 Jahren*.

Fig. 9. Gibbon male Nippy on 31 Mar. 2004, at an estimated age of 56 years. Photo: Pauline Wirihana. – *Das Gibbon-Männchen Nippy am 31 März 2004, im geschätzten Alter von 56 Jahren*.

Fig. 10. Gibbon male Nippy on 28 Aug. 2006, at an estimated age of 58 years. Photo: Wellington Zoo. – *Das Gibbon-Männchen Nippy am 28 Aug. 2006, im geschätzten Alter von 58 Jahren*.

Fig. 11. Gibbon male Nippy in foraging tray on 18 July 2007, at an estimated age of 59 years. Photo: probably by Pauline Wirihana. – *Das Gibbon-Männchen Nippy in seiner Futterkiste am 18 Juli 2007, im geschätzten Alter von 59 Jahren*.

Although Nippy's teeth were very worn down by 1996, he was still able to catch and eat fully able sparrows (e.g. in Jan. 2001, and Feb. 2008).

On 14 August 2001, Graeme Strachan (personal communication to TG) reported that "Nippy's condition usually got worse in cold weather. He got a chill several weeks ago and although he has recovered he is spending a lot of time now inside next to his heater and is not very active. During previous winters we have been concerned about his making it through to summer but being the gibbon that he is he has always bounced back. We have had some warm winter weather but he rarely sings, so caretakers are understandingly concerned about his future."

Nippy's thin arms suggested age-related muscle loss (Fig. 10), but the thin aspect of his arms may also have been influenced by fur loss. Nippy was much more agile in warmer weather. This was most likely a reaction to his low body mass and very little subcutaneous fat tissue. He clearly seeked warm and sheltered places in his outside area.

Nippy sang less often than in his younger days, but he still occasionally produced his long and loud solo song bouts. His activity levels varied from day to day. Sometimes he just rested in the sun and the next day he could be very active and vocalizing (Strachan, 2001). His songs could still be heard occasionally as late as 4 April 2008, when he produced a song bout of 30 minutes duration at noon.

Tape-recordings of three of Nippy's song bouts dating from 1974, 2001 and 2008, respectively, were available for analysis. Two phrases from each song bout are shown in Fig. 12. The three song bouts differ significantly in several time and frequency variables (Table 1). Due to variation in recording devices, poor recording quality, and the small sample size available for analysis, it is not clear what caused the differences. Causes could be Nippy's age, context of the song bout, recording equipment, or random variability among Nippy's vocal output.

Nippy was named after his passion for biting people. Numerous people have been bitten by the in-

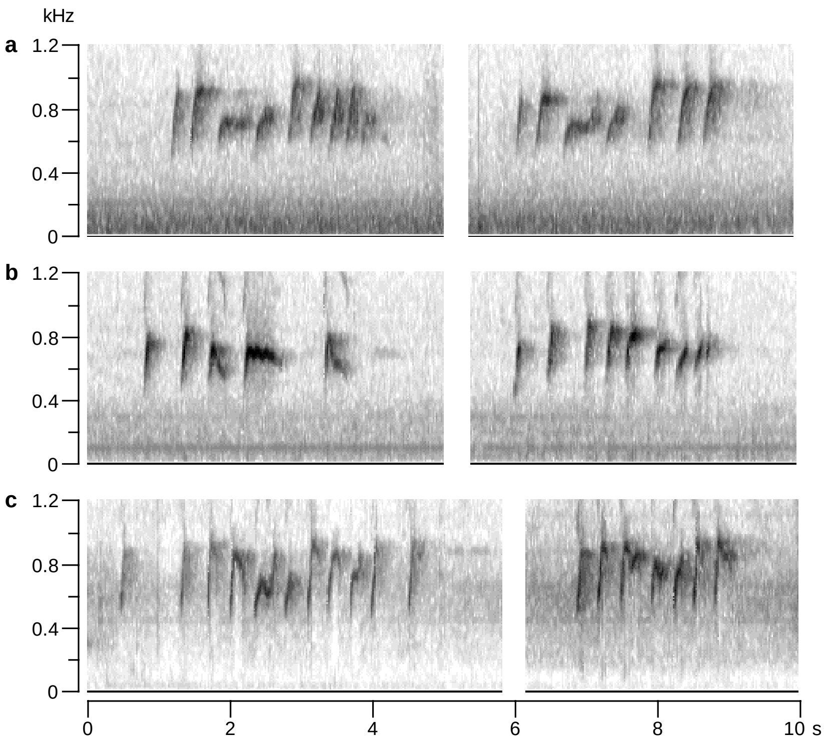

Fig. 12. Sonagrams of two fully developed short phrases each from three solo song bouts of the adult gibbon male Nippy. The song bouts were tape-recorded (a) c.1974, (b) Aug. 2001, and (c) 4 Aug. 2008. – *Sonagramme von je zwei voll ausgeprägten Strophen aus drei Solo-Gesängen des adulten Männchens Nippy. Das Datum der Tonaufnahmen ist circa 1974 (a), August 2001 (b), und 4. August 2001 (c).*

Table 1. Variables measured in sonagrams of three solo song bouts of adult male Nippy, and results from statistical comparison among the three recordings. Values shown include mean ± standard deviation, range (in parentheses), and sample size (i.e. number of analysed phrases). – *Verschiedene Variablen, die an Sonagrammen von Gesangsstrophen des Männchens Nippy bestimmmt wurden. Von den Messwerten sind Mittelwert ± Standardabweichung, Spannweite (in Klammern) und Anzahl ausgewertete Strophen angegeben. Die zwei letzten Spalten der Tabelle liefern die Resultate der statistischen Vergleiche zwischen den drei Tonaufnahmen*.

Variable	**Recording date of song bout**			**ANOVA**	**Significant Bonnferroni / Dunn *post-hoc* tests (p < 0.017)**
	c.1974	**Aug. 2001**	**4 Aug. 2008**		
Lowest frequency of phrase (Hz)	467±31 (401-519) n = 10	366±19 (328-400) n = 20	385±45 (326-442) n = 8	p < 0.0001	1974 *vs*. 2001 1974 *vs*. 2008
Highest frequency of phrase (Hz)	997±27 (936-1027) n = 10	1071±41 (1000-1157) n = 20	996±31 (922-1008) n = 8	p < 0.0001	1974 *vs*. 2001 2001 *vs*. 2008
Frequency range of phrase (Hz)	530±45 (466-599) n = 10	703±35 (643-778) n = 20	589±68 (490-682) n = 8	p < 0.0001	1974 *vs*. 2001 1974 *vs*. 2008 2001 *vs*. 2008
Main frequency of phrase (Hz)	828±80 (668-894) n = 10	708±48 (681-818) n = 20	610±61 (506-689) n = 8	p < 0.0001	1974 *vs*. 2001 1974 *vs*. 2008 2001 *vs*. 2008
Number of notes (without inspiration notes)	8.0±2.2 (5-11) n = 10	4.9±1.3 (3-8) n = 20	8.4±4.0 (4-15) n = 8	p < 0.0001	1974 *vs*. 2001 2001 *vs*. 2008
Phrase duration (s)	2.9±0.6 (1.5-3.3) n = 10	2.8±0.7 (1.8-4.7) n = 20	3.7±1.4 (1.6-4.7) n = 8	p < 0.0001	1974 *vs*. 2008
Notes / second	3.7±0.9 (2.2-5.5) n = 10	1.9±0.4 (1.3-3.0) n = 20	3.0±0.8 (2.2-4.7) n = 8	p < 0.0001	1974 *vs*. 2001 1974 *vs*. 2008

famous Nippy but as time passed, Nippy's habit mellowed, and from the time he barely had any front teeth remaining (Fig. 6), his nips were not as effective as they once had been (Anonymous, 2004; NZPA, 2004).

Nippy's body weight was determined on 19 July 2003 to be 5 kg. Since then, his weight diminished slightly (18 Mar. 2004: 5 kg, 6 Sep. 2004: 4.68 kg, 23 Oct. 2007: 4.75 kg, 21 Nov. 2007: 4.75 kg, 19 Aug. 2008: 4.71 kg, 26 Aug. 2008: 4.735 kg).

In January 2003, it was first noticed that Nippy's hearing had deteriorated, and his deafness seemed more pronounced in 2004. Quite often he either did not hear when spoken to or if he did hear and the speaker was not in Nippy's view it was necessary to make more noise, such as banging on the cage mesh, to get his attention.

One of us (KG) first assessed Nippy in March 2003. At that point, he was a geriatric non-human ape and showed the typical symptoms of age related involuntary weight loss, muscle atrophy and worn teeth. There was a distinct dextro-convex thoracic scoliosis (= lateral, right curvature in the upper region of the spine) which made him appear bent and small (Fig. 13).

He had bilateral entropium (inversion of both eyelids) which caused chronic production of discharge from both eyes. Entropium is commonly seen in old animals and humans and is usually produced by a increasing relaxation of the smooth muscle around the eyes. In newspaper photographs published in June 1987 (Anonymous, 1987), Nippy's eyes still look healthy and seemingly without entropium (Fig. 3).

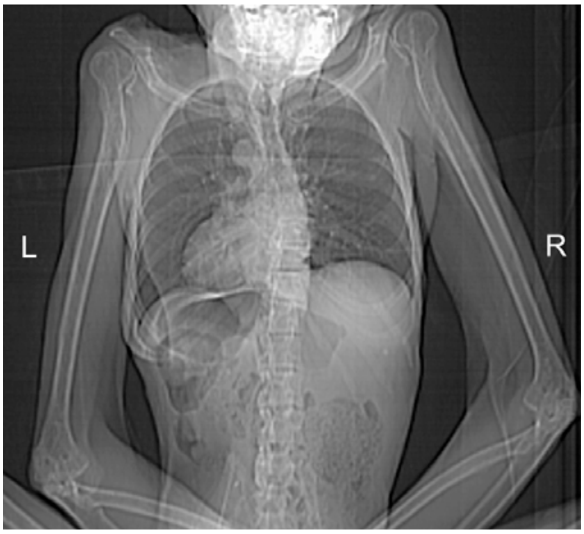

Fig. 13. Computer tomography scan of the chest of male *H. muelleri* Nippy, on 24 Sep. 2003, showing dextro-convex scoliosis of the vertebral column. – *Computer-Tomographie des Brustbereichs des Gibbon-Männchens Nippy vom 24. Sept. 2003. Die rechts-konvexe Skoliose der Wirbelsäule ist deutlich zu erkennen*.

In September 2003 Nippy underwent a computer tomography (CT) scan which revealed erosion of the medial wall of the left orbit and an abnormal soft tissue mass which extends to the medial canthus (inside corner of the eye) where it measures approximately 8 mm (Fig. 14). The erosion had well defined sclerotic margins, suggesting that it was an indolent process. An aspiration of the cavity contained a bacterial culture of *Pseudomonas aeruginosa* which was resistant to relevant antibiotics. Nippy had been on and off systemic antbiotics for a long time, and after consultation with human and veterinary specialists, the Wellington Zoo veterinary and curatorial team decided to discontinue the treatments because it was unlikely that they would reach the abscess inside the bone in sufficient dosages. Surgical treatment was not selected because of fear that his facial bones might collapse. Nippy was put on a supportive treatment with additional high caloric and palatable food items as well as medication. Daily he received ¼ of an effervescent Berocca tablet (vitamin supplement; Bayer), 0.25ml Alpha-Lactulose (contains laculose 3.34 mg/5ml), ¼ Echinacea tablet and 1 tablespoon of Nutrigel (high calorie nutritional support; Ethical Agents Ltd.).

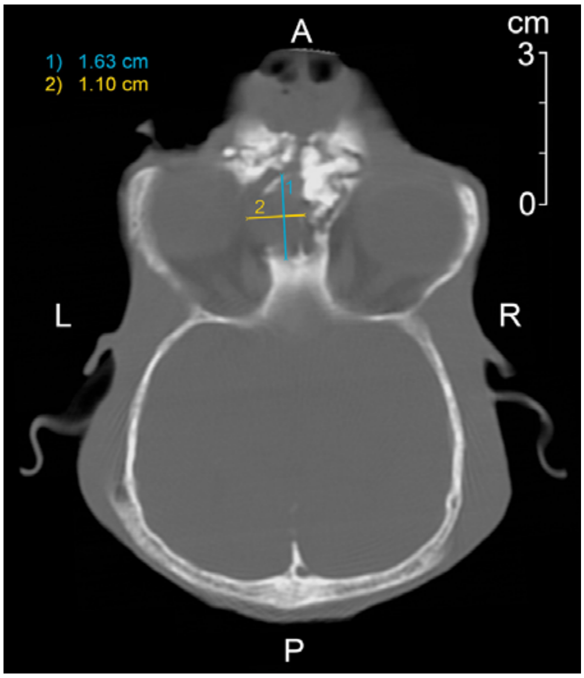

Fig. 14. Computer tomography scan of the head of gibbon male Nippy, on 24 Sep. 2003, showing erosion of the medial wall of the left orbit. – *Computer-Tomographie des Kopfes des Gibbon-Männchens Nippy vom 24. Sept. 2003. Sie zeigt die Auflösung der medialen Wandung der linken Augenhöhle.*

Longevity and body weight

The longevity of the genus *Hylobates*, as represented by the male *H. muelleri* appears to be exceptionally high. Fig. 15 shows the relationship between log body weight and log longevity in various groups of primates. Each dot represents one genus.

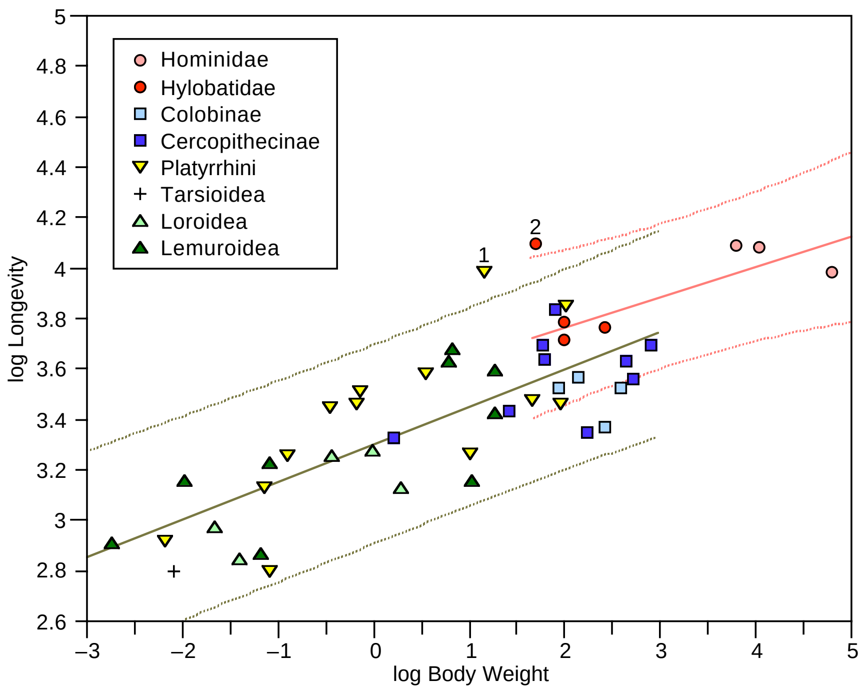

Fig. 15. Relationship between body weight and longevity in various groups of primates. Each dot represents one genus. The linear regressions were calculated under exclusion of the genus *Hylobates*. The regression line and confidence curves apply to non-hominoid primates. The one to the right applies to hominoids. The two variables are significantly correlated ($p < 0.001$, and $p < 0.05$, respectively). Only two samples lie outside (and above) their respective confidence limits: *Cebus* (1) and *Hylobates* (2). – *Beziehung zwischen Körpergewicht und Langlebigkeit bei Primaten. Jeder Punkt stellt eine Primatengattung dar. Die Gattung* Hylobates *wurde bei den Regressionsberechnungen ausgeklammert. Die linke Regressionsgerade mit* Konfidenzintervallen *gilt für die Nicht-Menschenaffen, die rechte für die Menschenaffen. Die beiden Variablen sind statistisch signifikant miteinander korreliert* (p < *0.001, beziehungsweise* p < *0.05). Nur zwei Stichproben liegen ausserhalb (und oberhalb) der Konfidenzintervalle: Die Kapuzineraffen, Gattung* Cebus *(1) und die Kleingibbons, Gattung* Hylobates *(2).*

A first linear regression with confidence limits was calculated for non-hominoid primates. The two variables are highly correlated ($p < 0.001$). Only one genus (*Cebus*, capuchin monkeys) appears to lie outside the confidence limits that cover 95% of all data points. Primates of the genus *Cebus* appear to exhibit a higher longevity than other primates of this body size. An extension of the regression line and limits to the right would also include all apes except gibbons of the genus *Hylobates*. The latter also exhibit a higher longevity than what should be expected from their body weight.

A second regression line with confidence limits was calculated for hominoid primates. The genus *Hylobates* was excluded from this calculation. Again, the two variables are correlated ($p < 0.05$). As the regression line for apes is based on solely six data points, it should be considered with caution. An extension of the regression line and confidence limits to the left would also include the genus *Cebus*, but again exclude the genus *Hylobates*.

In a regression line with confidence limits including all primate genera (graph not shown), the genera *Cebus* and *Hylobates* both are situated above the confidence limits.

Although the total number of apes living in captivity is not known, numeric proportions among the species or genera can be estimated by using the numbers of animals of each genus that are currently living in ISIS (International Species Information System) member institutions (Table 2).

Table 2. Numbers of apes of each genus kept in ISIS institutions.[1] – *Die Individuenzahl der Menschenaffen, aufgegliedert nach Gattung, die in ISIS-Mitgliedsinstitutionen gehalten werden*.

Genus	Numbers in captivity
Small apes, Hylobatidae:	
Hoolock gibbon (*Hoolock*)	0
Crested gibbon (*Nomascus*)	284
Siamang (*Symphalangus*)	324
Dwarf gibbon (*Hylobates*)	682
Great apes, Hominidae:	
Orangutan (*Pongo*)	654
Gorilla (*Gorilla*)	767
Chimpanzee (*Pan*)	1'357

[1] Source: http://app.isis.org/abstracts/abs.asp [consulted on 23 July 2008]

Among ape genera, log longevity correlates significantly with log numbers in captivity ($p = 0.034$), as shown in Fig. 16. For this calculation, the genus *Hoolock* was excluded, as it was not kept in any of the ISIS member institutions and the logarithm for a population size of zero is not defined. The correlation between log Longevity and log Numbers in captivity is even more significant ($p < 0.0001$) if non-hominoid genera are included as well (plot not shown).

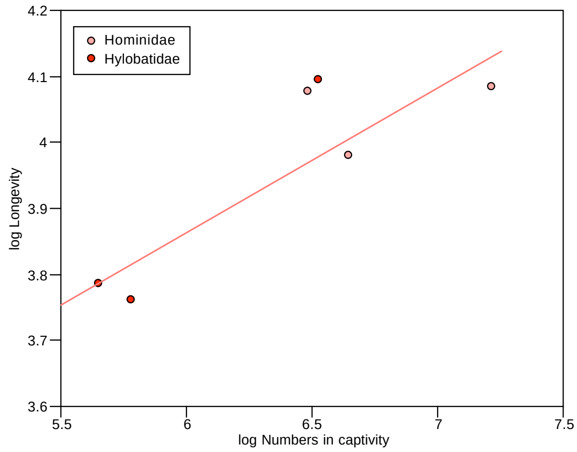

Fig. 16. Relationship between longevity and numbers of apes of each genus kept in ISIS institutions (as listed in Table 1). The linear regression was calculated under exclusion of the genus *Hoolock*, because its captive population size of zero could not be converted to a logarithm. The two variables are significantly correlated ($p = 0.034$). – *Beziehung zwischen Langlebigkeit und in ISIS-Mitgliedsinstitutionen gehaltenen Individuen der Menschenaffen. Die Gattung* Hoolock *wurde nicht berücksichtigt, da der Logarithmus für eine Populationsgrösse von Null nicht definiert ist. Die beiden Variablen sind statistisch signifikant miteinander korreliert (*p *= 0.034)*.

A comparison of log Body weight with log Numbers in captivity does not reveal a significant correlation among primate genera ($p > 0.05$).

Discussion

With an estimated age at death of 60 years, Nippy the Mueller's gibbon (*Hylobates muelleri*) attained one of the highest known life spans among non-human primates, including the great apes. Currently the proven longevity record for a living ape is held by a male chimpanzee, Kongo, who is still alive at 60 years and 7 months (Weigl, 2009). As shown by the results of this study, the genus *Hylobates* exhibits a higher longevity than what can be expected for a primate of this body weight.

How can this result be interpreted? (1) The genus *Hylobates* could be truly exceptional, similar to the genus *Cebus*. (2) The seemingly elevated longevity of *Hylobates* could be an artefact based on coincidence or on sampling size. These two interpretations will be briefly evaluated below.

The reason why *Cebus* exhibits an elevated longevity is poorly understood. This genus is also exceptional among Neotropical primates in a number of other characteristics, including longer period of skeletal development, extended nursing duration, delayed onset of puberty, elevated brain size (Fedigan and Rose, 1995; Fragaszy and Bard, 1997; Harvey *et al*., 1987), high propensity for tool using behaviour, and a high variety of cognitive abilities (Fragaszy *et al*., 1990; Ottoni and Mannu, 2001; Visalberghi, 1990, 1997; Westergaard and Fragaszy, 1987). Within this set of specialities, an elevated longevity would be plausible at least. So far, no such specialities, as compared to other hominoid primates, have been reported for the genus *Hylobates*, so far. An elevated longevity for this gibbon genus would seem to be more surprising than for the genus *Cebus*.

Alternatively, the result for the genus *Hylobates* could just be an artefact. For instance, Nippy could just be a singularity, an incredibly "tough" gibbon that is not representative of its genus.

Sample size could also have influenced the result. Longevity of genera or taxonomic groups that are rarely kept, or that are difficult to keep, in captivity, such as members of the Loroidea, Tarsioidea or the Colobinae, may be under-explored. This may be one reason why most or all data points of these primate groups lie below the regression line (Fig. 15).

Among gibbons, the genus *Hylobates* is by far the best represented in captivity. It may, therefore, be no coincidence that the highest longevity is found in a member of this genus. Consequentially, the lowest longevity value is reported for the genus *Hoolock*, which is by far the least represented in captivity (Table 2).

Because we found reported longevity in primates to be correlated with the number of individuals of each genus in captivity (Fig. 16), it is plausible to assume that considerably higher longevity may eventually be recorded for gibbon genera other than *Hylobates* as more data become available. This may not necessarily apply, however, to genera of the great apes. To judge by their body weight, they should exhibit higher longevity than all of the small apes, but the longevity value reported in this study for the genus *Hylobates* is one of the highest known longevity values among non-human primates including the great apes. However, the numbers of great apes kept in captivity are of similar size or even considerably larger than those of *Hylobates*, which is the most common gibbon genus in captivity (Table 2). As a result, a lack of data does not appear to be responsible for the relatively modest longevity in great apes like orangutans (*Pongo*) and gorillas (*Gorilla*), as compared to the small apes. An increase in sample size may produce only a moderate increase in the longevity recorded for these great ape genera.

If zoos had a preference for keeping primates of large body size, this would also produce a correlation between population size and longevity. Such a preference, however, was not found in our study. We found no correlation between log Body weight and log Numbers in captivity. This suggests that the observed correlation between the captive population size and longevity does not result from a preference of zoos for large-sized primates.

In summary, *Hylobates* is too long-lived for its body weight, and a similar result may eventually be confirmed for the other gibbon genera when larger numbers of individuals are surveyed. Traditionally, the great apes are identified as the long-lived apes (Carey and Judge, 2000), but when adjusted for body size, longevity in small apes appears to be even more exceptional. Elevated longevity is a feature gibbons appear to share with the Neotropical monkeys (*Cebus*) and humans, but how and why the feature evolved in gibbons will require further investigation.

Acknowledgements

We are grateful to Neil Price, Richard Weigl and Pauline Wirihana for photographs, to Graeme Strachan for providing two tape-recordings of Nippy's song bouts, and to Frank Coles and Graeme Strachan for helpful information on Nippy's previous history. Michael Biggs kindly provided a photograph from the Wellington City Archives. We thank Richard Weigl for information on chimpanzee "Cheeta" and Karin Isler for helpful discussions regarding the statistical analyses.

References

Adams, G. (2008). Monkey business: Has Cheeta been cheated out of a star on Hollywood's Walk of Fame? *The Independent* (Internet, 20 June 2008) www.independent.co.uk/arts-entertainment/film-and-tv/features/monkey-business-has-cheeta-been-cheated-out-of-a-star-on-hollywoods-walk-of-fame-850942.html

Anderson, L. (1987). Zoo announces record gibbon birth. *AAZPA (American Association of Zoological Parks and Aquariums) Newsletter* **28**(9): 25.

Anonymous (1949a). Zoo animals arrive. *The Evening Post, Wellington*, 2 Dec. 1949.

Anonymous (1949b). New feature for the zoo. *Evening Post, Wellington*, 28 Dec. 1949.

Anonymous (1950). Zoo animals cost a lot. *The Evening Post, Wellington*, 5 April 1950.

Anonymous (1953). Wonderful show at zoo. *The Evening Post, Wellington*, 3 Dec. 1953.

Anonymous (1954a). Percy Pelican is oldest pet at Wellington zoo. *New Zealand Free Lance*, 8 Sep. 1954, pp. 18-20.

Anonymous (1954b). From the Binturong down… Zoo represents big investment. *The Evening Post, Wellington*, 12 Dec. 1954.

Anonymous (1987). Old man of the zoo. *The Evening Post, Wellington*, 2 June 1987.

Anonymous (1997). It's a gibbon's life: Nippy turns 50. *CNN interactive*, 4 Dec. 1997 (Internet): www.cnn.com/EARTH/9712/04/gibbon.bday/

Anonymous (1999). Nippy happy in his nifty fifties. *Absolutely Positively Wellington, W.C.C. Newsletter*, Dec. 1999, p. 8.

Anonymous (2002). Title unknown. *The Dominion Post, Wellington*, 14 Oct. 2002.

Anonymous (2004). Old buddies (Internet report, *Wellington Zoo*, 2 Dec. 2004) www.wellingtonzoo.com/inform/news/nr1101935522.html

Anonymous (2005). Older and wiser… but still Nippy. *The Dominion Post, Wellington*, 15 Sep. 2005.

Anonymous (2008a). *ARKS specimen report for Wellington Zoo / M10*. Unpublished, consulted: 24 July 2008.

Anonymous (2008b). A fond farewell to Nippy the gibbon. *Absolutely Positively Wellington*, Oct. 2008, p. 16. Internet: www.wellington.govt.nz/publications/pdfs/2008-10-apw.pdf

Anonymous (2008c). Nippy no more. (Internet report, 2 Sep. 2008) www.stuff.co.nz/4678286a11.html

Anonymous (2008d). Nippy the gibbon put down. *TVNZ*, 2 Sep. 2008 (Internet): http://tvnz.co.nz/view/page/423466/2052837

Anonymous (2008e). Nippy, oldest known gibbon in captivity, dies. *Earth Times*, 2 Sep. 2008 (Internet): www.earthtimes.org/articles/show/229343,nippy-oldest-known-gibbon-in-captivity-dies.html

Anonymous (2008f). R.I.P. Nippy. *Wellington Zoo*, 23 Sep. 2008 (Internet): www.wellingtonzoo.com/net/news/article.aspx?id=9

Anonymous (2008g). World's oldest gibbon passes away. (Internet report, 2 Sep. 2008) http://3news.co.nz/News/HealthNews/Worldsoldestgibbonpassesaway/tabid/420/articleID/69709/cat/58/Default.aspx

Anonymous (2008h). Zoo’s oldest resident dies. *Scoop*, 2 Sep. 2008 (Internet): www.scoop.co.nz/stories/AK0809/S00021.htm

Austad, S. N., and Fischer, K. E. (1992). Primate longevity: Its place in the mammalian scheme. *American Journal of Primatology* **28**: 251-261.

Carey, J. R., and Judge, D. S. (2000). *Longevity records: Life spans of mammals, birds, amphibians, reptiles, and fish*, Odense University Press, Odense, 241 pp.

Charif, R. A., Waack, A. M., and Strickman, L. M. (2008). *Raven Pro 1.3 user’s manual*, Cornell Laboratory of Ornithology, Ithaca, NY, x+313 pp.

Fedigan, L., and Rose, L. (1995). Interbirth intervals in sympatric monkeys in Central America. *American Journal Primatology* **37**: 9-24.

Flower, S. S. (1931). Contributions to our knowledge of the duration of life in vertebrate animals. - V. Mammals. *Proceedings of the Zoological Society, London* **1931**: 145-234.

Fragaszy, D. M., and Bard, K. 1997. Comparison of development and life history in *Pan* and *Cebus*. *International Journal of Primatology* **18**: 683-701.

Fragaszy, D. M., Visalberghi, E., and Robinson, J. G. (1990). Variability and adaptability in the genus *Cebus*. *Folia Primatologica* **54**: 114–118.

Geissmann, T. (1991). Reassessment of age of sexual maturity in gibbons (*Hylobates* spp.). *American Journal of Primatology* **23**: 11-22.

Geissmann, T. (1998). Body weight in wild gibbons (Hylobatidae). In *Abstracts, XVIIth Congress of the International Primatological Society, August 10-14, 1998, abstract no. 282*, University of Antananarivo, Madagascar.

Geissmann, T., and Anzenberger, G. (2009). Hormonal correlates of the ovarian cycle in the yellow-cheeked crested gibbon (*Nomascus gabriellae*), and a review of ovarian cycles in gibbons (Hylobatidae). *Gibbon Journal* **5**: 61-73.

Geissmann, T., and Orgeldinger, M. (1995). Neonatal weight in gibbons (*Hylobates* spp.). *American Journal of Primatology* **36**: 179-189.

Gordon, A. D. (2006). Scaling of size and dimorphism in primates II: Macroevolution. *International Journal of Primatology* **27**: 63-105.

Harvey, P. H., Martin, R. D., and Clutton-Brock, T. H. (1987). Life histories in comparative perspective. In Smuts, B. B., Cheney, D. L., Seyfarth, R. M., Wrangham, R. W., and Struhsaker, T. T. (eds.), *Primate societies*, University of Chicago Press, Chicago and London, pp. 181-196.

Henderson, R. (2002). Oldest swinger in the zoo reaches 55. *The Evening Post, Wellington*, 30 Nov. 2002.

Hill, R. (1999). Still monkeying around. *Cook Strait News, Wellington*, 29 or 30 Nov. 1999, p. 5.

Ikram, A. (2008). Farewell Nippy the gibbon. *3News.co.nz* 3 Sep. 2008 (Internet): www.3news.co.nz/TVShows/Sunrise/AlisSmashHits/AlisBlog/tabid/834/articleID/69795/cat/592/Default.aspx

Jones, M. L. (1962). Mammals in captivity – Primate longevity. *Laboratory Primate Newsletter* **1**(3, July 1962): 3-13.

Jones, M. L. (1968). Longevity of primates in captivity. *International Zoo Yearbook* **8**: 183-192.

Jones, M. L. (1979). Longevity of mammals in captivity. *International Zoo News* **129** (26/3): 16-26.

Jones, M. L. (1982). Longevity of captive mammals. *Der Zoologische Garten (N.F.)* **52**: 113-128.

Ling, J. (2008). Farewell Nippy – Gibbon but not forgotten. *Dominion Post*, 3 Sep. 2008 (Internet): www.stuff.co.nz/dominionpost/4678570a23918.html

Martinez, M. (2008). Old but still a swinger. *Chicago Tribune*, 6 July 2008 (Internet): www.chicagotribune.com/news/nationworld/chi-cheeta-letter_bdjul06,0,2325289.story?track=rss

Nagpal, S. (2008). Nippy, oldest known gibbon in captivity, dies. *TopNews.in*, 2 Sep. 2008 (Internet): www.topnews.in/nippy-oldest-known-gibbon-captivity-dies-263970

Nash, E. (2008). Exclusive: Hollywood chimp Cheeta gets star on Walk Of Fame. *Mirror.co.uk: Celebs*, 6 July 2008 (Internet): www.mirror.co.uk/celebs/latest/2008/07/08/exclusive-hollywood-chimp-cheeta-gets-star-on-walk-of-fame-89520-20635735/

Neate, R. (2008). Cheeta, Tarzan star and world's oldest chimpanzee, hopes for Hollywood recognition. *Telegraph.co.uk.*, 8 July 2008 (Internet): www.telegraph.co.uk/news/newstopics/celebritynews/2267639/Cheeta,-Tarzan-star-and-world's-oldest-chimpanzee,-hopes-for-Hollywood-recognition.html

NZPA (2004). A special friendship *The Sidney Morning Herald*, 4 Dec. 2004 (Internet): www.smh.com.au/news/Unusual-Tales/A-special-friendship/2004/12/03/1101923341888.html

Ottoni, E. B., and Mannu, M. (2001). Semifree-ranging tufted capuchins (*Cebus apella*) spontaneously use tools to crack open nuts. *International Journal of Primatology* **22**: 347-358.

Puschmann, W., and Federer, E. (2008). Ein neuer Fertilitätsnachweis bei einer hoch betagten Schimpansin und Anmerkungen zum Höchstalter von *Pan troglodytes*. *Zoologischer Garten N.F.* **77**: 182-185.

Rosen, R. D. (2008). Lie of the jungle. *Washington Post*, Sunday, 7 Dec. 2008; Page W14. (Internet): www.washingtonpost.com/wp-dyn/content/article/2008/11/25/AR2008112500939.html?hpid=features1&hpv=national

Sacher, G. A. (1975). Use of zoo animals for research on longevity and aging. In *Research in Zoos and Aquariums*, pp. 191-197. National Academy of Sciences, Washington, D.C.

Strachan, G. (2001). The oldest living Mueller's gibbon (*Hylobates muelleri*). *The Gibbon's Voice* 5 (1, Dec. 2001): 4-5.

Suzuki, J., Kato, A., Maeda, N., Hashimoto, C., Uchikosi, M., Mizutani, T., Doke, C., and Matsuzawa, T. (2003). Plasma insulin-like growth factor-1, testosterone and morphological changes in the growth of captive agile gibbons (*Hylobates agilis*) from birth to adolescence. *Primates* **44**: 273-280.

Visalberghi, E. (1990). Tool use in *Cebus*. *Folia Primatologica* **54**: 146–154.

Visalberghi, E. (1997). Success and understanding in cognitive tasks: A comparison between *Cebus apella* and *Pan troglodytes*. *International Journal of Primatology* **18**: 811-830.

Weigl, R. (2005). *Longevity of mammals in captivity; from the living collections of the world. A list of mammalian longevity in captivity*, Kleine Senckenberg-Reihe 48. E. Schweizerbart'sche Verlagsbuchhandlung Stuttgart, 214 pp.

Weigl, R. (2009). Cheeta – the world's oldest chimpanzee? *International Zoo News* **56** (1) (Jan./Feb. 2009, No. 370): 24-25.

Wellington City Council (2004). Presentation of long service award. In: *Wellington city council, Ordinary meeting, minutes, Wednesday 6 Oct. 2004*, pp. 3-5. Downloadable from www.wellington.govt.nz/haveyoursay/meetings/title/Council/2004/06Oct1730/pdf/20041006minutes.pdf

Westergaard, G. C., and Fragaszy, D. M. (1987). The manufacture and use of tools by capuchin monkeys (*Cebus apella*). *Journal of Comparative Psychology* **101**: 159-168.

Wikipedia contributors (2008). Cheeta. *Wikipedia, The Free Encyclopedia* (accessed 13 Aug. 2008): http://en.wikipedia.org/w/index.php?title=Cheeta&oldid=230275189

Zusammenfassung

Langlebigkeit von Gibbons (*Hylobatidae*)

Ein Langlebigkeits-Rekord von 60 Jahren bei einem Müllers Gibbon (*Hylobates muelleri*) im Zoo von Wellington (Neuseeland) wird vorgestellt. Dies scheint der zweitälteste nicht-menschliche Primat zu sein, der bisher bekannt ist, aber sein hohes Alter ist noch bemerkenswerter, wenn man es zur Körpergrösse dieser Gibbons in Beziehung setzt. Dass die Langlebigkeit von Säugetieren mit ihrer Körpergrösse korreliert, ist bekannt. Eigentlich sollte man daher erwarten, dass die Gattungen der Gibbons oder kleinen Menschenaffen aufgrund ihres geringeren Körpergewichtes durchgehend niedrigere Langlebigkeiten aufweisen als die grossen Menschenaffen. Die hier vorgestellte Langlebigkeit der Gibbon-Gattung *Hylobates* kehrt diesen erwarteten Befund aber zumindest für zwei Gattungen grosser Menschenaffen auf den Kopf: Orang-Utans (*Pongo*) und Gorillas (*Gorilla*).

Die Resultate dieser Studie zeigen weiter, dass es auch eine signifikante Korrelation zwischen der Populationsgrösse einer Primaten-Gattung in Gefangenschaft und deren maximaler bekannter Lebensdauer gibt. Ein Vergleich zwischen der Langlebigkeit und der Zahl der Tiere in Gefangenschaft lässt vermuten, dass die bisher belegte Langlebigkeit der Gibbon-Gattungen *Hoolock*, *Nomascus* und *Symphalangus* deshalb niedriger ist als diejenige der Gattung *Hylobates*, weil *Hylobates* viel häufiger in Gefangenschaft gehalten wird und daher die Langlebigkeit auf einer grösseren Datenmenge basiert. Die Resultate dieser Studie lassen vermuten, dass in Zukunft bei allen Gibbon-Gattungen erhöhte Langlebigkeit relativ zu ihrem Körpergewicht gefunden wird, wenn grössere Datenmengen zur Verfügung stehen. Bei grossen Menschenaffen, von denen bereits jetzt grössere Gefangenschafts-Populationen als bei *Hylobates* vorliegen, dürfte eine weitere Vergrösserung der Datenmengen eine bescheidenere Korrektur der beobachteten Langlebigkeit zur Folge haben als für die meisten Gibbon-Gattungen.