



# Population history of chimpanzees introduced to Lake Victoria's Rubondo Island

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## Abstract

Between 1966 to 1969, Bernhard Grzimek (Frankfurt Zoological Society, FZS) introduced chimpanzees (*Pan troglodytes*) previously held in European institutions to Rubondo Island in Lake Victoria in Tanzania. Earlier publications report various numbers of released animals and that all founders originated from West Africa. We revise these assumptions through consultation of archived FZS records and genetic analyses of surviving descendants. Accordingly, 17 chimpanzees were transported to Africa in four waves, with male–female ratios of 3:8, 1:0, 1:0 and 2:2; one female died in transit. Thus, 16 chimpanzees were released in total. FZS and studbook records allocate a West African provenance to only 19% of the founders and a generic “Africa” origin to 56%. Still, studbook records render it unlikely that any of the founders were captive-born. In addition, our genetic analyses based on biological samples from the current descendants trace the geographical origin of their ancestors back to West Africa (*P. t. verus*) and Central Africa (*P. t. troglodytes*). Based on counts of individuals and night nests, we estimate that the population, since 1969, grew to around 35 individuals in 2014 (annual increase 3.3%). Thus, chimpanzees released onto a large forested island free from predators or hunting pressure, habitat destruction and conspecific competition can form a self-sustaining island population without human support.

**Keywords** Great ape · *Pan troglodytes* · Reintroduction · Release · Hybrids · Rewilding

## Introduction

As is true for other non-human primates, wild populations of chimpanzees (*Pan troglodytes*) are declining due to anthropogenic disturbance (Lonsdorf et al. 2010). Subspecies currently recognised are *P. t. verus* (West Africa), *P. t. troglodytes* (Central Africa), *P. t. schweinfurthii* (East Africa) and *P. t. ellioti* (Cameroon and Nigeria). Chimpanzee diet varies across populations, with ripe fruit being the staple. To minimize competition, communities split up into smaller foraging parties of typically 2–10 members (fission–fusion).

An estimated 345,000–470,000 wild chimpanzees remain (Humle et al. 2016); several thousand are held in institutions outside Africa (Carlsen and de Jongh 2014) and in African sanctuaries (Hughes et al. 2011). Introductions of ex-captive chimpanzees into the wild have had mixed survival outcomes (Hannah and McGrew 1991), as suitable habitat not occupied by other apes and safe from hunters or conflict with humans is scarce (see Beck 2019 for review of primate releases). These problems are mitigated on some islands (Pryde and Cocklin 1998), albeit introduced animals might need to be provisioned with food.

In this respect, a historic island introduction of chimpanzees initiated by the German veterinarian Bernhard Grzimek (1909–1987) is of particular interest. Grzimek, from 1945 to 1974 director of the Frankfurt Zoological Garden, envisioned to turn the island of Rubondo in the Tanzanian part of Lake Victoria in East Africa into a “sanctuary for threatened animals” (Grzimek 1970: 14). A well-known nature conservationist, Grzimek emphasized the tourism potential of a future Rubondo Island National Park to the authorities of the newly independent Tanzania (Schürmann 2017). Gazetted a game reserve in 1965, the island became a national park in

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1977. Bolstered by Grzimek's status as honorary trustee of Tanganyika National Parks and his presidency of the Frankfurt Zoological Society (FZS), various large mammals were transported to the island between 1963 to 1973. Of these non-endemic taxa, elephant (*Loxodonta africana*), giraffe (*Giraffa camelopardalis*), suni antelope (*Neotragus moschatus*) and black-and-white colobus (*Colobus abyssinicus*) still survive to this day (JNM and VS, pers. obs.).

The introductions also included ex-captive chimpanzees transported from Europe (Grzimek 1970). Various follow-up studies documented their fate, with at times contradictory statements about numbers and sex of the released apes. Information about their provenance is considered “patchy and incomplete” (Petrášová et al. 2010: 922), although it is commonly maintained that all apes were “wild-born in several West African countries” (e.g., Huffman et al. 2008: 221).

Given this context, our paper has several objectives (some of which dovetail with research needs identified by Huffman et al. 2008). (i) To reconstruct provenance, the number and sex of the founder individuals is revisited in historical records including those of FZS archives. (ii) This information is compared with previous reports to identify potential contradictions and inaccuracies. (iii) The founders' geographical origin is determined via mitochondrial DNA analyses. (iv) The increase in population size over half a century since the founders' release is evaluated via counts of night nests and direct observations of chimpanzees. (v) The current population's fission–fusion patterns are gauged to assess if they coincide with natural variation. (vi) The implications of this historic release experiment are discussed in relation to future chimpanzee conservation efforts.

## Methods

### Review of historical records

The first Rubondo chimpanzee release was documented by Grzimek during a 1966 episode on his prime-time West German TV series *Ein Platz für Tiere* (“A Place For Animals”), followed by printed narratives. Post-release, various surveys and research efforts resulted in published outputs (Table 1), which, however, contain disparate statements about provenance, numbers, age and sex of the released animals, as well as their subsequent fate. Based on translations of German sources by co-authors VS and FS, we present a detailed overview on the Rubondo founders in the results section.

### Field data

Lead-author JNM conducted research on Rubondo from April to August 2012 and October 2012 to March 2014

(Msindai 2018). Rubondo Island National Park (02° 18' 10.3" S, 31° 51' 26.9" E), located in the south-western part of Lake Victoria, Tanzania, encompasses 237 km<sup>2</sup> at 1100–1486 m a.s.l. (Fig. 1). Today, only rangers and their families along with tourist lodge staff inhabit the island—120 people (M. Mwishawa, Rubondo Chief Park Warden, pers. comm. to JNM). A liana-rich mixed evergreen and semi-deciduous forest covers 80–90% of the island. The mean minimum and maximum temperature are respectively 16 °C and 29 °C. Mean annual rainfall is 1200 mm (with peaks from March to May and October to December).

Chimpanzees were tracked by a team of 2–8 people consisting of JNM, local field assistants, foreign researchers, volunteers and at times senior author VS. Trackers communicated via radio. Tracking was typically conducted from 07:00 to 16:00 from April to August 2012 and 06:00–18:00 from October 2012 to March 2014, for a total of 547 individual days. Fieldwork included sampling chimpanzee shed hairs (from within night nests), food wadges (discarded) and faeces (collected on the day of defecation, from underneath night nests or during the day following a sighting). Roughly 2–10 g of faecal or food-wadger material was placed in 50 ml tubes filled with 96–99% ethanol (25 ml). Hairs were placed in empty tubes. For all samples, we recorded time, date, location, longitude, latitude and collector ID. Samples were stored at ambient temperature. Locations of chimpanzee sightings and sleeping platforms (night nests) were logged via a Garmin GPSMAP 62 device.

While frequency and length of direct observations increased throughout the study, the apes were not habituated to human presence. Events from when the first chimpanzee became visible until the last disappeared out of sight were labelled as an *encounter*. A new encounter was logged when the previous observation had occurred at least 3 h prior or at a distance of 5 km from the current sighting. On most occasions, the team did not find the chimpanzees again on the same day. Size of day parties was defined as the number of chimpanzees travelling together that were seen and counted. Size of night parties was defined via the number of nests in a cluster, i.e., not further away than 50 m from another nest. Trees with nests were marked to avoid double-counts. To not erroneously allocate night nests built on different days to the same cluster, we only considered abandoned new nests, i.e., those built the night before—identified from freshly broken foliage and the presence of faeces or urine underneath.

To infer population size, we used the maximum sizes of day and night parties (in this case including nests dated to have been built within the past week). However, infant chimpanzees do not construct their own nests and sleep with their mothers. The proportion of infants in well-studied communities averages 23.6% (range 11.2–38.1%; Hughes et al. 2011). We thus added 24% to the largest night nest count, to arrive at a figure for the minimum population size. In

**Table 1** Publications, surveys and research projects about the Rubondo apes. FZS = Frankfurt Zoological Society

Period (yyyy-mm-dd)	Name	Institution, Position (activity)	Output
1966	Bernhard Grzimek	FZS (project initiator)	Grzimek 1966a, 1966b, 1966c, 1967, 1969, 1970, 1988
1966-Jun–mid-1967	Sinclair Dunnett	Game warden, Mwanza (irregular chimpanzee surveys)	
1966-Jul–1968-Mar	Ulrich Kade	FZS (German forester volunteer, surveys)	Kade 1967
1969-Feb–1971-Jan	Hans Sönksen	ditto	
1971-Jan–1972-Sep	Wolfgang Brockmann	ditto	
1972-Sep–1975	Wolfgang Matschke	ditto	
1974-Jan-10–Apr-01	Gustl Anzenberger	FZS (surveys)	Anzenberger 1977
1978–1984	Monica Borner, Markus Borner	FZS (tasked to develop newly declared Rubondo Island National Park)	Borner 1980, 1985, 1988
1994	Guido Müller	Univ. of Zurich, Switzerland (socio-ecological research)	Müller and Anzenberger 1995
1996–2002	Paula Robinson, Johan Robinson	FZS (chimpanzee habituation attempts)	Robinson and Robinson 1998 [Unpublished report]
1998-Apr-30–May-08	Anne Pusey	Duke Univ., USA (survey)	Pusey 1998 [Unpublished report]
1998	D. Ommaney	FZS (habituation attempts)	Ommaney 1998 [Unpublished report]
2000-Sep-02–16	Akiko Matsumoto-Oda	Primate Research Inst., Kyoto Univ., Japan (research)	Matsumoto-Oda 2000
2002–2008 (intermittently)	Michael Huffman	Primate Research Inst., Kyoto Univ., Japan (research)	Huffman et al. 2008
2002–2004	Liza Moscovice	Univ. of Wisconsin–Madison, USA (PhD research)	Moscovice 2004, Hasegawa et al. 2005, Moscovice 2006 [PhD thesis], Moscovice et al. 2007, 2010
2003–2008 (intermittently)	Klara Petrželková, Lucia Bobakova, Vladimír Mazoch, Mwanahamissi Issa Mapua	Inst. of Vertebrate Biology, Academy of Sciences, Czech Republic (parasitology research)	Petrželková et al. 2006, 2010; Petrášová et al. 2010, 2011
2003–2008 (intermittently)	Taranjit Kaur, Jatinder Singh	Virginia Polytechnic Inst., USA (ape health monitoring)	
2012-Apr–2014-Mar	Josephine N. Msindai	Univ. College London, UK (PhD research)	Msindai et al. 2015, Msindai 2018 [PhD thesis]
2014–2017	Felix Schürmann	Univ. of Erfurt in Gotha, Germany (archival work in Germany and Tanzania)	Schürmann 2016, 2017
Since 2016		Tanzania National Parks Authority (habituation attempts)	

*ditto* information from table cell above applies

addition, we calculated day and night party sizes (median, mean, range, standard deviation [sd]) to compare the fission–fusion dynamics of the self-formed Rubondo population to natural populations.

## Genetics

Utilizing the biological samples, the subspecies identity (matrilines) of Rubondo chimpanzees was explored under direction of co-author CR with assistance by JNM. DNA was extracted in 2015, 12–36 months after collection, from a total of 201 samples (faeces  $n = 196$ , hair  $n = 4$ , food wadges  $n = 1$ ), using the First-DNA-All-Tissue-Kit (Gen-ial) and

following the standard protocol for stool samples with minor modifications as outlined in Kalbitzer et al. (2016). After extraction, DNA concentration was measured with a NanoDrop ND-1000 spectrophotometer (peqlab) and then DNA extracts were stored at  $-20\text{ }^{\circ}\text{C}$ .

A 460–500 bp-long fragment of the mitochondrial control region spanning the hypervariable region I (HVI) was amplified and sequenced using the published primers L 15997 (5′–CACCATTAGCACCCAAAGCT–3′) and H16498 (5′–CCTGAAGTAGGAACCAGATG–3′) in a large-scale study (Mitchell et al. 2015). Polymerase chain reaction (PCR) amplifications were performed in a total volume of 30  $\mu\text{l}$  containing 1 U BioTherm Taq 5000 (GeneCraft), 1X

**Fig. 1** Rubondo Island National Park, Lake Victoria, Tanzania



reaction buffer, 0.16 mM of each dNTP, 0.33  $\mu$ M of each primer, 0.6 mg/ml BSA and ca. 100 ng total DNA. To check for cross-sample contamination, we always ran two negative (no-template) controls along with ten samples. Thermal cyclor conditions consisted of 94 °C for 2 min, followed by 40–50 cycles of 94 °C for 1 min, 58 °C for 1 min and 72 °C for 1 min, followed by 72 °C for 5 min. PCR performance was checked on 1% agarose gels. Excised PCR

products were purified with the QIAquick Gel Extraction Kit (Qiagen) and then sequenced on an ABI 3130x L sequencer (Applied Biosystems) using the BigDye Terminator 3.1 Cycle Sequencing Kit (Applied Biosystems) and both amplification primers. Obtained sequence electropherograms were visually inspected with 4Peaks 1.8 software (nucleobytes.com/4peaks/) and sequences were assembled in SeaView 4.5.4 (Gouy et al. 2010).

Haplotypes were determined using the ElimDupes online server ([hiv.lanl.gov](http://hiv.lanl.gov)), and taxon assignment was conducted via BLAST search ([blast.ncbi.nlm.nih.gov](http://blast.ncbi.nlm.nih.gov)) using 100% query cover. Molecular sex determination of samples was conducted using a universal PCR-based sexing system in which fragments of the X-chromosomal DDX3 gene and of the Y-chromosomal DDY3 gene are simultaneously amplified (Ferreira da Silva et al. 2018). PCR reactions were performed in a total volume of 30 µl containing 1 U BioTherm Taq 5000 (GeneCraft), 1X reaction buffer, 0.16 mM of each dNTP, 0.33 µM of each primer, 0.6 mg/ml BSA and ca. 100 ng total DNA. Thermal cycler conditions comprised 94 °C for 2 min, followed by 50 cycles of 94 °C for 30 s, 54 °C for 30 s and 72 °C for 30 s, followed by 72 °C for 5 min. PCR products were then size-separated on 2.5% agarose gels and sex was determined via visual inspection of the gels. To monitor contamination, for each batch of ten samples, two negative (non-template) controls were applied.

## Results

### Founder population: reconstruction via historical records

Our archival research reconstructs the provenance of chimpanzees released onto Rubondo as well as events surrounding their transport to the island (Table 2) which in turn enabled us to identify missing information and critically evaluate previously published statements. We ascertained that the project centres around 17 chimpanzees (male–female ratio 7:10) likely born between 1954 to 1960 and previously held captive in Europe, of which 16 were actually released (7:9). The apes were transported to Africa in four successive waves: (i) 3:8 on board a freighter (1 female died en route), (ii) 1:0 via plane, (iii) 1:0 via plane and (iv) 2:2 via plane. Releases took place 23 June 1966 to 30 June 1969. Publications agree on the number and composition of the last three releases. Statements about the first release are often incorrect, partly because one animal died during the journey. Interestingly, Grzimek (1966a) reports the release of 11 animals, but later states he “dispatched ten large chimpanzees” (e.g., Grzimek 1970: 13)—perhaps trying to cover up the fact that one did not survive. Subsequently, instead of 16 released animals, Borner (1980, 1985, 1988) erroneously reports 17—a mistake cited or otherwise perpetuated in, e.g., Müller and Anzenberger (1995: 12), Matsumoto-Oda (2000), Huffman et al. (2008), Petrášová et al. (2010), Moscovice et al. (2007) and Msindai et al. (2015).

Previous publications also misrepresent the sex ratio of the first wave as 4:7, instead of 3:8 (which would include the deceased female, e.g., Borner 1985; Müller and Anzenberger

1995; Huffman et al. 2008). Moreover, while correctly reporting 10 released animals in the first wave, their sex ratio is wrongly stated as 4:6 instead of 3:7 by Schürmann (2017: 17), because an unnamed male was in fact a female (Kathrin, no. 9; cf. Table 2). Finally, Müller and Anzenberger (1995: 12) report 12 animals in the first wave (4:8, including the animal that died in transit). However, our recent archival work could not confirm the existence of an unnamed male (no. 9) in Müller and Anzenberger’s table which is, therefore, excluded from our summary.

Previous publications also conjecture the apes’ provenance, seemingly carried over from one source to the next. Thus, several reports explicitly state that all released apes were born in the wild in Africa (Borner 1985: 152; Pusey 1998: 2; Matsumoto-Oda 2000: 16; Moscovice et al. 2007: 3; Huffman et al. 2008: 222; Msindai et al. 2015). A more particular origin from “West Africa” is also made explicit (Pusey 1998: 2; Matsumoto-Oda 2000: 16; Petrášová et al. 2010: 923; Huffman et al. 2008: 222), while some sources mention the specific countries Guinea, Cote d’Ivoire, and Sierra Leone (Matsumoto-Oda 2000: 16; Huffman et al. 2008: 222).

Our archival research located origin records for 13 of the 17 dispatched chimpanzees, while there is no origin record for four apes. For 9 of the 13 with origin records, “Africa” or “probably Africa” is indicated. For four individuals, a specific country was noted (1 × Sierra Leone, 2 × “probably” Guinea, 1 × “probably” Cote d’Ivoire).

Importantly, one individual of “known” origin—female Joséphine (“probably” from Guinea)—died in transit, leaving just 3/16 (19%) of the founders with a designated regional origin (nos. 2, 4, 9, Table 2). However, even those designations only indicate the country from where they were shipped out and not necessarily, where they were born. By exclusion, we are almost certain that all founders were wild-born, because the studbook (Carlsen and de Jongh 2014) lists only a handful of chimpanzees born in European zoos before the 1970s and these did not include nos. 14–17 in Table 2.

The 17 apes were collected from across seven countries (Sweden, Denmark, Netherlands, France, Germany, Switzerland, Austria), where they had been kept between 3.5 months and up to 9 years by zoos (15 animals), circuses (4) or animal traders (3), often changing hands between owners. All but one (kept with orangutans) were housed with at least one other chimpanzee. Some endured solitary periods under severe spatial restrictions. Female Jette, as a 7-year-old, gave birth to two infants without raising them. When travelling to Africa, nine chimpanzees were familiar with at least one other captive conspecific, but the others were not. Contrary to previous statements (Grzimek 1970: 13f), our compilation (Table 2) indicates that none of the 16 released survivors had reached full adulthood of 13–15 years (cf. Haverkamp

Table 2 Provenance of the founder population of Rubondo chimpanzees

No	Release date on Rubondo (yyyy-mm-dd)	Name (studbook number)	Sex	Origin	Date of birth	Captivity (place, duration)	Captivity (housing condition)	Acquisition for Rubondo release	Approximate age upon release (years)
1	1966-Jun-23	Simba	F	Africa	1956–1957	Since 1960 at <i>Furuvisparken</i> , Furuvis, Sweden (6 years)	Furuvis: housed with other chimpanzees; no offspring; no serious illness recorded	Donated jointly by Gottfried Fridh of Stockholm and <i>Furuvisparken</i>	9
2	1966-Jun-23	NR	F	Sierra Leone	NR	Directly from Africa to animal trader <i>Jabria</i> , Herderwij, Netherlands (3.5 months)	Kept with 2 similar-aged chimpanzees; weight on departure to Rubondo 17 kg; no serious illness recorded	Bought from <i>Jabria</i>	4
3	[Died 1966-Jun-06 in transit from heat stroke after stopover at Port Said]	Joséphine	F	Probably Guinea	1957	<i>Parc zoologique et botanique de Mulhouse</i> , Mulhouse, France (when 18 months old)	Joséphine and Schilla arrived 1964 and were kept in improvised enclosure ("Notunterkunft") without outdoor access; no serious illness recorded; weak physical and psychological condition	Presumably exchanged	[8]
4	1966-Jun-23	Schilla	F	Probably Guinea	1957–1958	<i>Parc zoologique et botanique de Mulhouse</i> , Mulhouse, France	ditto	Exchanged	8–9
5	1966-Jun-23	Lillemor (10760)	F	Africa	ca. 1960	Garden Society of Gothenburg ( <i>Trädgårdsföreningen</i> ), Sweden, ca. 1962 to <i>Borås Djurpark</i> (aka <i>Berggren Zoo Park</i> ), Sweden	Probably kept with other chimpanzees	Gift from <i>Borås Djurpark</i>	6
6	1966-Jun-23	Ricky (10769)	M	Africa	ca. 1960	ditto	Kept with other chimpanzees in small cage; weak physical and psychological condition	ditto	6

Table 2 (continued)

No	Release date on Rubondo (yyyy-mm-dd)	Name (studbook number)	Sex	Origin	Date of birth	Captivity (place, duration)	Captivity (housing condition)	Acquisition for Rubondo release	Approximate age upon release (years)
7	1966-Jun-23	Lola	F	Probably Africa	ca. 1955	Kobenhavn Zoo, Denmark, handed over by officers of ship MS Norden (1957–Nov-20), probably directly from Africa	Ca. 2 years old on arrival; always kept with other chimpanzees	Gift from Kobenhavn Zoo	11
8	1966-Jun-23	Bastian	M	Africa	ca. 1962	Bought from animal trader Krag (Kopenhagen), delivered to Kobenhavn Zoo, Denmark (1963–Jun-25)	Ca. 1 year old upon arrival; 1 month in solitary confinement, afterwards kept with 2 orangutans	ditto	4
9	1966-Jun-23	Kathrin (Vienna, Austria) resp. Caroline (Basle, Switzerland)	F	Probably Ivory Coast	ca. 1956-Jun	From residence of Prof. Hans Huggel, Ivory Coast (1 year), sent directly to Zoo Basel, Switzerland (1958–Apr-25); <i>Tiergarten Schönbrunn</i> , Vienna, Austria (1963–Jul-29); <i>Frankfurt Zoo</i> (1966–May-11)	Huggel-residence Ivory Coast: kept with human children and other non-ape primates; Basel: kept with slightly older female chimpanzee and similar-aged orangutans and gorillas; Vienna: at first together with chimpanzee male, then separated	Bought from <i>Tiergarten Schönbrunn</i>	10
10	1966-Jun-23	Kathy	F	Probably Africa	ca. 1958–1959	Taken over from a Danish captain named Hansen; <i>Zoo Gelsenkirchen</i> , Germany (1961–Jun-15 – Dec-17); (Zoo?) Dortmund, Germany (1961–Dec-17 – 1965–Nov-18); afterwards <i>Zoo Duisburg</i> , Germany	Gelsenkirchen, Dortmund: kept with other chimpanzees; Dortmund (Duisburg?): Kathy and Robert kept together	Bought from animal trading zoo <i>Tierpark Schloss Kreckling</i> (Tierhandelszoo Konrad Müller)	5–7

Table 2 (continued)

No	Release date on Rubondo (yyyy-mm-dd)	Name (studbook number)	Sex	Origin	Date of birth	Captivity (place, duration)	Captivity (housing condition)	Acquisition for Rubondo release	Approximate age upon release (years)
11	1966-Jun-23	Robert	M	Probably Africa	1958–1959	ditto	ditto	ditto	5–7 ("fully grown" according to Grzimek 1966a, b, c, 1970); (likely shot dead after attacking game wardens; Borner 1985: 152)
12	1966-Oct-19	Jimmy (10676; name = Demo)	M	Africa	ca 1958	First in circus, then in Zoo Herford, Germany (from 1962); 1966-Feb-01 Zoo Frankfurt, Germany	Herford: kept with 2 female chimpanzees; blind left eye due to corneal injury	From Zoo Frankfurt	7 or 8; (shot dead 1968-Oct after attacking volunteer and game wardens; Grzimek 1970: 37)
13	1968-Jan	Jimmy [sic] (10693)	M	Africa	ca 1958	Tierpark Lübbesche, Germany; Zoo Frankfurt 1967-Oct-27	NR	ditto	10
14	1969-Jun-30	Peggy	F	NR	ca. 1960	Acquired from animal trader Krag (Kopenhagen) by Zoo Wuppertal, Germany, in 1961 (ca. 8–9 years in captivity)	NR	Gift from Zoo Wuppertal	9
15	1969-Jun-30	Jette	F	NR	1960	Donated to Zoo Wuppertal, Germany, by animal trainer Konzelmann of Tierpark Hagenbeck (Hamburg) once found too big for circus performance (≥ 8 years in captivity)	Zoo: Jette, Bobby, Jeff kept as one group; Jette gave birth in 1967 and 1968, did not raise her infants	ditto	9
16	1969-Jun-30	Bobby	M	NR	1959–1960	ditto	ditto	ditto	9–10
17	1969-Jun-30	Jeff	M	NR	1959–1960	ditto	ditto	ditto	9–10

NR no record; *ditto* information from table cell above applies

Data compiled from: (i) Grzimek 1966a, 1970; (ii) FZS records obtained by Gustl Anzenberger in 1973 (Müller and Anzenberger 1995); (iii) Schürmann 2017; Table 2; (iv) archival records obtained by co-author FS: Institut für Stadtgeschichte, Frankfurt am Main (Zoologische Garten 197 and 212); FZS (Afrika 00001970, Rubondo 3, Keller Regal 01021; 00001976, Rubondo 1, Keller Regal 01019); (v) European chimpanzee studbook (Carlsen and de Jongh 2014)



et al. 2019). Instead, at ca. 4–11 years, they were juveniles or subadults (female mean 8.1, range 4–11; male mean 8.1, range 6–10).

The apes were released without any prior rehabilitation. While food was provisioned during the first 2 months, the released apes fed on natural vegetation early on (Kade 1967). For at least 11 months post-release, they slept in tree forks (ibid.), before constructing nests and becoming completely self-reliant (Borner 1985). All animals released in 1966 were still alive in April 1967 (Kade 1967). In 1968, male Jimmy (no. 12) was shot after having injured rangers (Grzimek 1970: 37), a fate likely shared (Borner 1985: 152) by male Robert (no. 11). The first two babies were seen in February 1968 (ibid.). In 1985, when at least two founder females were seemingly still alive, the population was estimated to be “at least 20” (ibid.). Anecdotal reports indicate that some founders survived for decades (Matsumoto-Oda 2000: 17).

### Taxon assignment using mitochondrial DNA (mtDNA) sequences

The taxon identity of the founder individuals was clarified via HVI sequences (491–492 bp) generated for 196 samples. Determined by molecular sexing, 116 derived from females, 79 from males, with 1 undetermined. Among these, we found four haplotypes. Using BLAST search, one was identified as *P. t. troglodytes* (haplotype troglodytesA) and three as *P. t. verus* (haplotypes verusA, verusB, verusC). Haplotype troglodytesA, found in 66 individuals (23 male, 43 female), differs in four positions (99.2% identity) from its closest related sequence in GenBank (*P. t. troglodytes*: JN191203.1) and in at least 13 positions (97.4% identity) from sequences of other *P. t. ssp.*. Haplotype verusA, found in 2 individuals (both female), is 100% identical to the *P. t. verus* sequence JN191232.1 and differs in at least 26 positions (94.7% identity) from other *P. t. ssp.*, while the verusB haplotype, found in 80 individuals (41 male, 38 female, 1 undetermined), differs from haplotype verusA and JN191232.1 in one position (99.8% identity) and from other *P. t. ssp.* in at least 27 positions (94.5% identity). The verusC haplotype, found in 48 individuals (15 males, 33 females), differs from its closest related sequence in GenBank (*P. t. verus*: FJ642360.1) in three positions (99.4% identity) and from other *P. t. ssp.* in at least 29 positions (94.1% identity).

In summary, 66.3% of samples (56 male, 73 female, 1 undetermined) derived from individuals with a *P. t. verus* haplotype and 33.7% of samples (23 male, 43 female) from individuals with a *P. t. troglodytes* haplotype.

### Population increase

Our reconstruction (cf. Table 2) ascertains that by late 1969, 14 chimpanzees inhabited the island, including nine females.

To estimate the 2012–2014 population, we relied on maximum recorded numbers on one day. As for direct sightings, on 24 July 2013, we encountered 28 apes, one large party of 26 apes in the island’s south and 12 aerial km away another 2 adults to the north. As for night nests, on 09 May 2013, we counted 28 nests in a single cluster in the island’s north. These were built sometime during the preceding week, because the cluster was not present during intensive surveys of that forest area a week prior. To these 28 nests, we add 24% to account for infants sleeping with their mothers (see “Methods”)—thus the island harbours a minimum of  $(28 + 6.7 =) 35$  chimpanzees.

### Party sizes

To compare with natural populations, we measured fission–fusion patterns between April 2012 to March 2014. Chimpanzees were directly observed on 146 occasions, equating to 0.2 instances/day (monthly median 4, mean 7, range 1–22). Encounter durations lasted from < 1 min to up to 10 h (median 15 min, mean 45 min,  $sd = 84$ ). A day party typically encompassed four individuals (median = 4, mean = 4, range 1–26,  $sd = 3$ ,  $n = 146$ ), with no significant variation across months (Kruskal–Wallis median test:  $\chi^2 = 20$ ,  $df = 20$ ,  $p = 0.458$ ). We also found 1224 nests in various stages of decay, of these 190 (16%) constructed the previous evening. For these new nests, we calculated night party sizes (median = 5, mean = 5, range = 1–19,  $sd = 4$ ,  $n = 38$ ; note that this count ignores non-nest-building immatures; see above). Single nests accounted for 24% of all clusters. There was no significant variation between months (Kruskal–Wallis median test:  $\chi^2 = 18$ ,  $df = 18$ ,  $p = 0.456$ ). We also found no significant difference between day and night party sizes (Spearman’s rho test,  $\rho = -0.065$ ,  $s = 1215$ ,  $p = 0.789$ ).

Of 195 sex-determined biological samples, 59.5% derived from females and 40.5% from males. Assuming that sampling was random, the 2014 population thus contained 21 females and 14 males.

## Discussion

### Geographical origin

Our archival work (cf. Table 2) corroborates that 16 chimpanzees were released (ratios male–female 3:7, 1:0, 1:0, 2:2; cf. Table 2). It is almost certain that all were wild-born in Africa, although records for only three (19%) place their (likely) origin in Sierra Leone, Cote d’Ivoire or Guinea. Even then, assumptions about the geographical origin of captive populations based on the site of purchase can be misleading. For example, the 35 founders of

the Rijswijk chimpanzee colony purchased from a dealer in Sierra Leone were presumed to originate from upper Guinea, until analyses of mtDNA revealed that two were *P. t. troglodytes* (Gagneux et al. 2001). Our genetic analyses provide a further cautionary tale about presumed origins. Thus, mtDNA sequencing of Rubondo chimpanzees revealed that the founders represented the West African *P. t. verus* (66% of samples) as well as Central African *P. t. troglodytes* (34%).

Mirroring the Rubondo situation, historical records for 3906 chimpanzees held in European institutions till 2014 for which subspecies were known ( $n=906$ ) display a clear preponderance of *P. t. verus* (85.1%) over *P. t. troglodytes* (13.2%), with near absence of *P. t. schweinfurthii* (1.4%) and *P. t. ellioti* (0.2%) (Carlsen and de Jongh 2014: 36). This points to the mainland interior along the Atlantic coast as the preferred area of capture for apes for the European market—a dynamic also reflected in the Rubondo population. The lack of *P. t. ellioti* might be due to a smaller alignment of the subspecies habitat with the coastline in Nigeria and Cameroon (Oates et al. 2009).

## Population growth

Successive population estimates arrived at figures of (i) “at least 20” individuals in 1983 (Borner 1988), (ii) 24–32 in 1994 (Müller and Anzenberger 1995: 65) and (iii) “27–35 in 2004 (Moscovice 2006: 27)”. Our own 2014 estimate of a minimum of 35 individuals is thus towards the conservative side. Still, if we apply this estimate, then a starting population of 14 in 1969 grew by 21 animals over the next 46 years. This equates to an increase of 150% or 3.3% per year. This compares favourably with other sites, where deaths exceed births. For example, for infants born reaching 10 years, the figure is only 21% in Taï, Cote d’Ivoire, and 45% in Gombe, Tanzania (Hill et al. 2001). Figures for infants reaching age 10 years for the few communities known to increase in size are 58% females and 50% males at Kanyawara, Uganda (Muller and Wrangham 2014), and 70% females and 82% males at Ngogo, Uganda (Wood et al. 2017).

A combination of advantageous conditions allowed the Rubondo population to grow (cf. also Huffman et al. 2008): (i) no large terrestrial carnivores; (ii) no lethal conflicts with conspecific communities; (iii) a likely lack of major disease outbreak; (iv) low levels of resource competition; and (v) protection from anthropogenic disturbance, with the natural forest cover intact. The founders found themselves in rather “paradisiacal” conditions, allowing for rapid growth. Importantly, founders did not face conspecific competitors—unlike what happened to 37 chimpanzees released by HELP-Congo upon whom resident apes inflicted severe injuries

leading to four deaths (Goossens et al. 2005). Instead, the Rubondo chimpanzees have 200 km<sup>2</sup> of forest at their sole disposal. This allows them to be highly selective in terms of foraging, seeking out preferred food trees, even those at low density (Moscovice et al. 2007; Huffman et al. 2008). Furthermore, elsewhere, dispersing females tend to delay reproduction due to stress when entering a new community (Walker et al. 2018). The Rubondo apes have not split into different communities, and females thus remain and breed in their familiar social unit. Additionally, in the absence of intergroup competition, the Rubondo apes might experience shorter inter-birth intervals and higher rates of offspring survival (Lemoine et al. 2020). Given evidence from captivity (Ely et al. 2005), hybrid vigour could have temporarily decreased mortality in early generations. On the other hand, the relatively small numbers of founder females could in the future lead to inbreeding depression (Hufmann et al. 2008).

## Fission–fusion dynamics

Our surveys revealed mean cluster sizes of five night nests, similar to the figure of 5.5 reported by Müller and Anzenberger (1995: 45). The mean day party size was four individuals. The latter is comparable to means reported for natural chimpanzee populations (e.g., 5: Kanyawara, Uganda; 6: Sonso, Uganda; 6: Gombe, Tanzania; 6: Mahale, Tanzania; 4: Bossou, Guinea; Boesch and Boesch-Achermann 2000). Correspondingly, a community size of 35 equates to a relative mean party size of 11%, again similar to elsewhere (e.g., 12%: Sonso, Uganda; 13%: Taï, Cote d’Ivoire; 11–16%: Gashaka, Nigeria; Boesch and Boesch-Achermann 2000; Sommer et al. 2004). The lack of monthly variation in party size might be related to the relatively mild degree of climatic seasonality on the island (Moscovice et al. 2007). Our inferred male–female sex ratio of 2:3 is likewise close to natural communities, where males experience higher mortality (e.g., 60% females, 2014/2015 at Tai-East community, Cote d’Ivoire, McCarthy et al. 2018; 56% females, 2016 at Ngogo, Uganda, Wood et al. 2017).

The fission–fusion and sex ratio dynamics of Rubondo chimpanzees therefore fall into the range of variation elsewhere. Thus, although the founders experienced life as a “wild” chimpanzee only briefly as infants, they and/or their descendants developed a sociality similar to natural populations. To which degree this development toward chimpanzee-typical pattern is brought about by inherited factors or environmental stimuli is currently unknown. Future research will hopefully ascertain similarities or dissimilarities with other wild populations in more detail, and thus also broaden our understanding of chimpanzee cultural diversity (Kühl et al. 2019).

## Lessons for future ape releases?

Current International Union for the Conservation of Nature (IUCN) guidelines recommend that different chimpanzee subspecies should not be released jointly, to preserve genetic diversity (Beck et al. 2007). However, it should be kept in mind that genetic testing only recently became possible and affordable, and taxonomy is notoriously subject to change. When Grzimek released the first chimpanzee cohort in Rubondo in 1966, the subspecies division of *Pan troglodytes* was only just taking hold in academic circles (Napier and Napier 1967).

Other historical releases of great apes also contained individuals not rooted in the introduction area (Beck 2019). For example, two orangutans set free in Tanjung Puting National Park were recently identified not as native *P. p. wurmbii*, but as *Pongo pygmaeus pygmaeus* (Banes et al. 2016). Given the long generation spans of apes, we do not yet know if and how hybridisation will influence the reproductive success, health and viability of the affected populations. The conservation value of hybrids is generally debated, and they are sometimes considered to be “impure” forms that threaten the survival of “pure” types (Biermann and Mansfield 2014). Future projects similar to the Rubondo release will certainly weigh such arguments more carefully.

When preparing to dispatch the first batch of chimpanzees to Rubondo, Grzimek became increasingly concerned about critics, should the mission go wrong. To safeguard himself, he began to portray the Rubondo releases as an “experiment” (Schürmann 2017). The apes were introduced without any prior rehabilitation or training in foraging or nest-building skills. Moderate critique of Grzimek’s modus operandi was formulated by Borner (1985). She pointed out that (i) there was no post-release follow-up of how the individuals did or did not adapt to their new homes; (ii) some individuals were psychologically and physical unfit for release, causing their death; (iii) the composition of the release parties was random, with most animals being unfamiliar with each other; (iv) the releases occurred with considerable time intervals. Although Grzimek’s ad hoc approach might have accepted some mortality as inevitable, sophisticated modern release protocols that include lengthy rehabilitation efforts likewise do not safeguard against fatalities (Goossens et al. 2005). In general, success or failure of releases is judged against numbers of animals that survive and adapt to a wild life. Thus, at the minimum, the story of the Rubondo apes demonstrates that at least some ex-captive chimpanzees have the capacity to survive and breed in the wild, unaided by further human assistance.

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## Compliance with ethical standards

**Conflict of interest** The authors declare that they have no conflict of interest.

## References

- Anzenberger G (1977) Ethological study of African carpenter bees of the genus *Xylocopa* (Hymenoptera, Anthophoridae). *Z Tierpsychol* 44:337–374
- Banes GL, Biruté MFG, Vigilant L (2016) Reintroduction of confiscated and displaced mammals risks outbreeding and introgression in natural populations, as evidenced by orangutans of divergent subspecies. *Sci Rep* 6:22026
- Beck BB (2019) Unwitting travellers: a history of primate reintroduction. Salt Water Media LLC, Berlin
- Beck B, Walkup K, Rodrigues M, Unwin S, Travis D, Stoinski T (2007) Best practice guidelines for the re-introduction of great apes. SSC Primate Specialist Group of the World Conservation Union, Gland Switzerland
- Biermann C, Mansfield B (2014) Biodiversity, purity, and death: conservation biology as biopolitics. *Environ Plann D* 32:257–273
- Boesch C, Boesch-Achermann H (2000) The chimpanzees of the Tai Forest: Behavioural ecology and evolution. Oxford University Press, Oxford
- Borner M (1980) Rubondo—ein Nationalpark mausert sich. *Das Tier* 10:6–9
- Borner M (1985) The rehabilitated chimpanzees of Rubondo Island. *Oryx* 19:151–154
- Borner M (1988) Translocation of 7 mammal species to Rubondo Island National Park in Tanzania. In: Nielsen L, Brown RD (eds) Translocation of wild animals. Wisconsin Humane Society, Caesar Kleberg Wildlife Research Institute, Milwaukee, pp 117–122
- Carlsen F, de Jongh T (2014) European studbook for the chimpanzee *Pan troglodytes*. Copenhagen Zoo, Frederiksberg
- Ely JJ, Dye B, Frels WI, Fritz JO, Gagneux P, Khun HH, Switzer WM, Lee DR (2005) Subspecies composition and founder contribution of the captive US chimpanzee (*Pan troglodytes*) population. *Int J Primatol* 67:223–241
- Ferreira da Silva MJ, Kopp GH, Casanova C, Godinho R, Minhós T, Zinner D, Bruford MW (2018) Disrupted dispersal and its genetic consequences: comparing protected and threatened baboon populations (*Papio papio*) in West Africa. *PLoS ONE* 13:e0194189
- Gagneux PMK, Gonder TL, Goldberg MPA (2001) Geneflow in wild chimpanzee populations: what genetic data tell us about

- chimpanzee movement over space and time. *Philos Trans R Soc Lond B* 356:889–897
- Goossens B, Setchell JM, Tchidongo E, Dilambaka E, Vidal C, Ancrenaz M, Jamart A (2005) Survival interactions with conspecifics and reproduction in 37 chimpanzees released into the wild. *Biol Conserv* 123:461–475
- Gouy M, Guindon S, Gascuel O (2010) SeaView version 4: a multiplatform graphical user interface for sequence alignment and phylogenetic tree building. *Mol Biol Evol* 27:221–224
- Grzimek B (1966a) Ein Platz für Tiere. TV episode channel, ARD, West-Germany
- Grzimek B (1966b) Apes travel from Europe to Africa. *Afr Wildl* 20:271–288
- Grzimek B (1966c) Operation chimpanzee: youngster would not leave us. *Sunday News, Tanzania*
- Grzimek B (1967) Operation chimpanzee: Giant chimp starts dancing. *Sunday News, Tanzania*
- Grzimek B (1969) Grzimek unter Afrikas Tieren: Erlebnisse Ullstein. Forschungsergebnisse, Beobachtungen
- Grzimek B (1970) Among animals of Africa. Stein and Day, New York
- Grzimek B (1988) Die Auswilderung von Schimpansen. In: Grzimek B (ed) Grzimeks Enzyklopädie Säugetiere, vol 2. Kindler, München, pp 482–485
- Hannah AC, McGrew WC (1991) Rehabilitation of captive chimpanzees. In: Box HO (ed) Primate responses to environmental change. Chapman and Hall, London, pp 167–186
- Hasegawa H, Ikeda Y, Fujisaki A, Moscovice LR, Petrželková KJ, Kaur T, Huffman MA (2005) Morphology of chimpanzee pinworms *Enterobius (Enterobius) anthropopithecii* (Gedoelst 1916) (Nematoda: *Oxyuridae*) collected from chimpanzees *Pan troglodytes* on Rubondo Island Tanzania. *J Parasitol* 91:1314–1317
- Havercamp K, Watanuki K, Tomonaga M, Matsuzawa T, Hirata S (2019) Longevity and mortality of captive chimpanzees in Japan from 1921 to 2018. *Primates* 60:525–535
- Hill K, Boesch C, Goodall J, Pusey A, Williams J, Wrangham R (2001) Mortality rates among wild chimpanzees. *J Hum Evol* 40:437–450
- Huffman MA, Petrželková KJ, Moscovice LR, Mapua MI, Bobakova L, Mazoch V, Singh J, Kaur T (2008) Introduction of chimpanzees onto Rubondo Island National Park Tanzania. In: Soorae PS (ed) Global re-introduction perspectives: Re-introduction case-studies from around the globe. IUCN/SSC Re-Introduction Specialist Group, Abu Dhabi, pp 213–216
- Hughes N, Rosen N, Gretskey N, Sommer V (2011) Will the Nigeria-Cameroon chimpanzee go extinct? Models derived from intake rates of ape sanctuaries. In: Sommer V, Ross C (eds) Primates of Gashaka. Socioecology and conservation in Nigeria's biodiversity hotspot, Springer, New York, pp 493–523
- Humle T, Maisels F, Oates JF, Plumtre A, Williamson EA (2016) *Pan troglodytes* (errata version published in 2018). IUCN Red List Threat Sp 26:29038584
- Kade U (1967) Ich lebe mit den Schimpansen am Viktoriasee. *Das Tier* 6:31
- Kalbitzer U, Roos C, Kopp GH, Butynski TM, Knauf S, Zinner D, Fischer J (2016) Insights into the genetic foundation of aggression in *Papio* and the evolution of two length-polymorphisms in the promoter regions of serotonin-related genes (5-HTTLPR and MAOALPR) in *Papionini*. *BMC Evol Biol* 16:121
- Kühl HS, Boesch C, Kulik L et al (2019) Human impact erodes chimpanzee behavioral diversity. *Science* 363:1453–1455
- Lemoine S, Preis A, Samuni L et al (2020) Between-group competition impacts reproductive success in wild chimpanzees. *Curr Biol* 30:312–318.e3
- Lonsdorf EV, Ross SR, Matsuzawa T (2010) The mind of the chimpanzee: ecological and experimental perspectives. University of Chicago Press, Chicago
- Matsumoto-Oda A (2000) Chimpanzees in the Rubondo Island National Park Tanzania. *Pan Africa News* 7:16–17
- McCarthy MS, Després-Einspenner M-L, Samuni L, Mundry R, Lemoine S, Preis A, Wittig R, Boesch C, Kühl HS (2018) An assessment of the efficacy of camera traps for studying demographic composition and variation in chimpanzees (*Pan troglodytes*). *Am J Primatol* 80:e22904
- Mitchell MW, Locatelli S, Ghobrial L et al (2015) The population genetics of wild chimpanzees in Cameroon and Nigeria suggests a positive role for selection in the evolution of chimpanzee subspecies. *BMC Evol Biol* 15:3
- Moscovice LR, Petrželková KJ, Mapua MI, Huffman MA, Snowdon CT, Mbago F, Kaur T, Singh J, Graziani G (2004) Role of lianas for introduced chimpanzees (*Pan troglodytes*) on Rubondo Island Tanzania. *Folia Primatol* 75:933
- Moscovice LR (2006) Behavioral ecology of chimpanzees (*Pan troglodytes*) on Rubondo Island Tanzania: habitat diet grouping and ranging at a release site. PhD Dissertation. University of Wisconsin-Madison, Wisconsin
- Moscovice LR, Issa MH, Petrželková KJ, Keuler NS, Snowdon CT, Huffman MA (2007) Fruit availability chimpanzee diet and grouping patterns on Rubondo Island Tanzania. *Am J Primatol* 69:487–502
- Moscovice LR, Mbago F, Snowdon CT, Huffman MA (2010) Ecological features and ranging patterns at a chimpanzee release site on Rubondo Island, Tanzania. *Biol Conserv* 143:2711–2721
- Msindai JN (2018) Chimpanzees of Rubondo Island: ecology and sociality of an introduced population. PhD Dissertation. University College London, London.
- Msindai JN, Sommer V, Roos C (2015) The chimpanzees of Rubondo Island: genetic data reveal their origin. *Folia Primatol* 86:327
- Müller G, Anzenberger G (1995) Chimpanzees (*Pan troglodytes*) of Rubondo Island, Tanzania. Anthropologisches Institut der Universität Zürich. (Pilot study, German with English summary). DOI: <https://doi.org/10.13140/RG.2.2.31713.12648>
- Muller MN, Wrangham RW (2014) Mortality rates among Kanyawara chimpanzees. *J Hum Evol* 66:107–114
- Napier JR, Napier PH (1967) A handbook of living primates. Academic, New York
- Oates JF, Groves CP, Jenkins PD (2009) The type locality of *Pan troglodytes vellerosus* (Gray 1862), and implications for the nomenclature of west African chimpanzees. *Primates* 50:78–80
- Ommaney D (1998) Chimpanzee status survey and habituation project: Progress report 1998. Frankfurt Zoological Society. Unpublished report
- Petrášová J, Modrý D, Huffman MA, Mapua MI, Bobáková L, Mazoch V, Singh J, Kaur T, Petrželková KJ (2010) Gastrointestinal parasites of indigenous and introduced primate species of Rubondo Island National Park, Tanzania. *Int J Primatol* 31:920–936
- Petrášová J, Uzlíková M, Kostka M, Petrželková KJ, Huffman MA, Modrý D (2011) Diversity and host specificity of blastocystis in syntopic primates on Rubondo Island Tanzania. *Int J Parasitol* 41:1113–1120
- Petrželková KJ, Hasegawa H, Moscovice LR, Kaur T, Issa M, Huffman MA (2006) Parasitic nematodes in the chimpanzee population on Rubondo Island Tanzania. *Int J Primatol* 27:767–777
- Petrželková KJ, Hasegawa H, Appleton CC, Huffman MA, Archer CE, Moscovice LR, Mapua MI, Singh J, Kaur T (2010) Gastrointestinal parasites of the chimpanzee population introduced onto Rubondo Island National Park Tanzania. *Am J Primatol* 72:307–316
- Pryde PR, Cocklin C (1998) Habitat islands and the preservation of New Zealand's avifauna. *Geogr Rev* 88:86–113
- Pusey A (1998) Rubondo chimp project. Unpublished report

- Robinson J, Robinson P (1998) Chimpanzee status survey and habituation project: Progress report 1998. Frankfurt Zoological Society. Unpublished report
- Schürmann F (2016) Rubondo und eine Reise dorthin. Der Feldaufenthalt in der Geschichtswissenschaft–und unter afrikanischen Wildtieren. In: Forschungsschwerpunkt Tier-Mensch-Gesellschaft (ed) Den Fährten folgen: Methoden interdisziplinärer Tierforschung. Transcript, Bielefeld, pp 133–153
- Schürmann F (2017) Heimkehr ins Neuland. Die erste Auswanderung von Schimpansen und ihre Kontexte im postkolonialen Tansania 1965–1966. In: Forschungsschwerpunkt ‘Tier-Mensch-Gesellschaft’ (ed) Vielfältig verflochten: Interdisziplinäre Beiträge zur Tier-Mensch-Relationalität. transcript, Bielefeld, pp 275–292.
- Sommer V, Adanu J, Faucher I, Fowler A (2004) The Nigerian chimpanzee (*Pan troglodytes vellerosus*) at Gashaka: 2 years of habituation efforts. *Folia Primatol* 75:295–316
- Walker KK, Walker CS, Goodall J, Pusey AE (2018) Maturation is prolonged and variable in female chimpanzees. *J Hum Evol* 114:131–140
- Wood BM, Watts DP, Mitani JC, Langergraber KE (2017) Favorable ecological circumstances promote life expectancy in chimpanzees similar to that of human hunter-gatherers. *J Hum Evol* 105:41–56

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