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Population Dynamics of Wild Bonobos (*Pan paniscus*) at Wamba

Takeshi Furuichi,[1,8] Gen'ichi Idani,[2] Hiroshi Ihobe,[3] Suehisa Kuroda,[4] Koji Kitamura,[5] Akio Mori,[6] Tomoo Enomoto,[7] Naobi Okayasu,[3] Chie Hashimoto,[3] and Takayoshi Kano[6]

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We analyzed population dynamics and birth seasonality of wild bonobos at Wamba, Democratic Republic of the Congo, based on 20 years of observations (1976–1996). Wamba Bonobo infant mortality is much lower than that reported for chimpanzees. This seemes to be related to several socioecological characteristics of bonobos: the use of abundant fruit and herbaceous foods, larger food patch size, female feeding priority, and the absence of infanticide. The mean interval between live births of 4.8 years is shorter than those reported for chimpanzees, and some females simultaneously carried and nursed two successive offspring. Mother-offspring conflicts, such as refusal of suckling attempts and interference with mothers' copulation, which are common in chimpanzees, are rare in Wamba bonobos. A birth peak seems to occur during the light rainy season from March to May, just after the season with the least rainfall. This timing of births is similar to those reported for chimpanzee populations, and might benefit both mother and offspring by maximizing the amount of time before the next dry season.

KEY WORDS: *Pan paniscus*; bonobo; demography; interbirth interval.

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[1] Laboratory of Biology, Meiji-Gakuin University, 1518 Kamikurata, Totsuka, Yokohama, 244 Japan.

[2] Hayashibara Museum of Natural Sciences, Okayama, Japan.

[3] Faculty of Science, Kyoto University, Kyoto, Japan.

[4] School of Human Cultures, The University of Shiga Prefecture, Shiga, Japan.

[5] Faculty of Humanity, Hirosaki University, Aomori, Japan.

[6] Primate Research Institute, Kyoto University, Aichi, Japan.

[7] School of Medicine, Tokai University, Kanagawa, Japan.

[8] To whom correspondence should be addressed.

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INTRODUCTION

Studies of bonobos have revealed many socioecological traits that may influence population dynamics. For example, unlike chimpanzees, female bonobos often resume estrus around one year after giving birth (Furuichi, 1989, 1992; Kano, 1989, 1992; Wrangham, 1993), which may shorten the interbirth interval. Furthermore, the abundant food resources and large food patches (Kano and Mulavwa, 1984; White and Wrangham, 1988; Kano, 1992; Malenky *et al.*, 1994) may influence infant mortality, age at sexual maturity, and longevity. However, information on the demography of wild bonobos is very limited compared to that for chimpanzees (Goodall, 1983; Sugiyama, 1984; Nishida *et al.*, 1990; Tutin, 1994).

We analyzed population data from a 20-year study of wild bonobos at Wamba, Democratic Republic of the Congo, from 1976 to 1996. Although preliminary analyses of earlier data indicated a different interbirth interval (Takahata *et al.*, 1996; Hashimoto, 1997), we present a fuller analysis of the latest data set.

The main study group had been provisioned for part of the year, and the additional food availability might have had some influence on the population dynamics. However, comparative data from unprovisioned groups in the same study area suggest that the influence is minimal, though the findings should be confirmed by observations of more unprovisioned groups in this and other study areas. In the meantime, Wamba has the longest-studied population, and the data are therefore invaluable for comparative studies of great ape behavioral ecology and the viability of wild bonobos.

MATERIALS AND METHODS

Field observation of wild bonobos began at Wamba, Zone de Djolu, Région de l'Equateur, in 1973 (Kuroda, 1979; Kano, 1992). One of the unit groups inhabiting this area, E group, was habituated through artificial provisioning, and all its members were individually identified by 1976. E group originally consisted of a southern subgroup and a northern subgroup. The two subgroups split between 1982 and 1983 into independent unit groups, E1 and E2 (Kano, 1982; Kitamura, 1983; Furuichi, 1987). In this paper, E1 refers both to the southern subgroup of E group and to the E1 unit group itself, and E2 refers to the northern subgroup of E group and, also, to the E2 unit group.

There are two rainy seasons and two relatively dry seasons that are based on monthly rainfall in the study area (Kano, 1992, Data for Djolu,

Fig. 8, p. 50). The light rainy season is from March to May, and the severe one is from September to November. The relatively dry seasons are from June to August and from December to February, the latter having less rainfall.

Due to financial restrictions, we conducted observations primarily between August and February (Kano *et al.*, 1994). We confirmed members of the study groups on January 1st of each year, or inferred them from observations nearest to that date. Researchers were absent from August 1991 to February 1994 due to a political disorder in Zaire (Kano *et al.*, 1994, 1996), except during a short visit in August 1992 to check members of study groups. We estimated membership on January 1st of 1993 and 1994 from our observations in August 1992 and February 1994, and from information given by field assistants who observed the study groups during our absence.

E1, the main subject of our study, was the focus of intensive behavioral observation, and was provisioned at two artificial feeding sites in the forest (Ihobe, 1992; Kano, 1992). Bonobos of this group occasionally visited the feeding sites to take sugar cane during the dry season from December to February. They usually spent a few hours per day at a feeding site, and each individual took 1–3 sticks of sugarcane. During the dry season from June to August, artificial food was mostly unavailable due to the absence of researchers. Bonobos rarely visited the feeding sites during the rainy seasons, apparently because they preferred to feed on abundant wild fruits in the forest (Kano and Mulavwa, 1984; Kano, 1992; Hashimoto *et al.*, 1998). During the rainy seasons, we sometimes offered a small amount of sugar cane in the early morning at sleeping sites, but it was often ignored.

E2 was provisioned with artificial food to a far lesser extent. Although we sometimes used sugarcane in order to confirm membership or interindividual relationships, we usually observed E2 without provisioning.

We recorded information on new births, immigration from other groups, and emigration or disappearance for E1 and E2. Insofar as possible, we recorded the presence of each individual on every observation day. Demographic data were available for all members of E1 throughout the study period (1976–1996). We determined matrilineal kin relationships in E1 by a combination of field observations and analysis of nucleotide sequences of mitochondrial DNA (Hashimoto *et al.*, 1996). We used data on E1 to analyze mortality, interbirth interval, and birth seasonality. We also used data for individually identified adult females of E2 in the analysis of interbirth intervals. However, we used no datum on E2 in other analyses because some of its members were not individually identified. Furthermore, we used no datum on E2 from 1990 due to the lack of continuous observation.

There are at least four other groups, P, B, K, and S, in the vicinity of these study groups (Kano, 1992), and, only P was partially habituated and had some individuals identified. Members of P sometimes appeared at the artificial feeding site, but not often enough for provisioning to have influenced their behavior. We referred to observations on this group to evaluate the influence of provisioning on E1.

Males and females ≤ 7 years old are called infants and juveniles. Individuals 8–14 years old are called adolescents, because females begin to transfer to nonnatal groups when they are around 8 years old. Individuals > 15 years old are called adults; researchers estimate that females first give birth at around 15 years (Hashimoto, 1997).

We computed the survival ratio for each age by dividing the number of individuals that survived to that age by the number at birth. We calculated yearly mortality for each age by dividing the number of individuals that had died since the previous age by the number of surviving individuals at that previous age.

RESULTS

Changes in Group Size

Figure 1 shows changes in size and composition of E1 from 1976 to 1996. Group size gradually increased from January 1976 to January 1987, so we refer to it as the growth period. Group size was rather stable from January 1987 to January 1991, so we refer to it as the stable period. During both growth and stable periods, members of E1 were free from poaching, with the exception of one adult male that was killed in 1984.

The stable period was followed by a political disorder, and group size rapidly decreased from January 1991 to January 1994. Some members may have been killed by poachers during the absence of researchers. We refer to this period as during the disorder. Researchers resumed frequent visits to the study site in 1994, and we refer to the period from January 1994 to January 1996 as after the disorder. Although some members were lost after the disorder, there is no evidence that they were victims of poaching.

Numbers of immigrations and emigrations of late juvenile or adolescent females are also in Fig. 1. Changes of group size due to these migrations are +0.18 individual per year during the growth period, –0.75

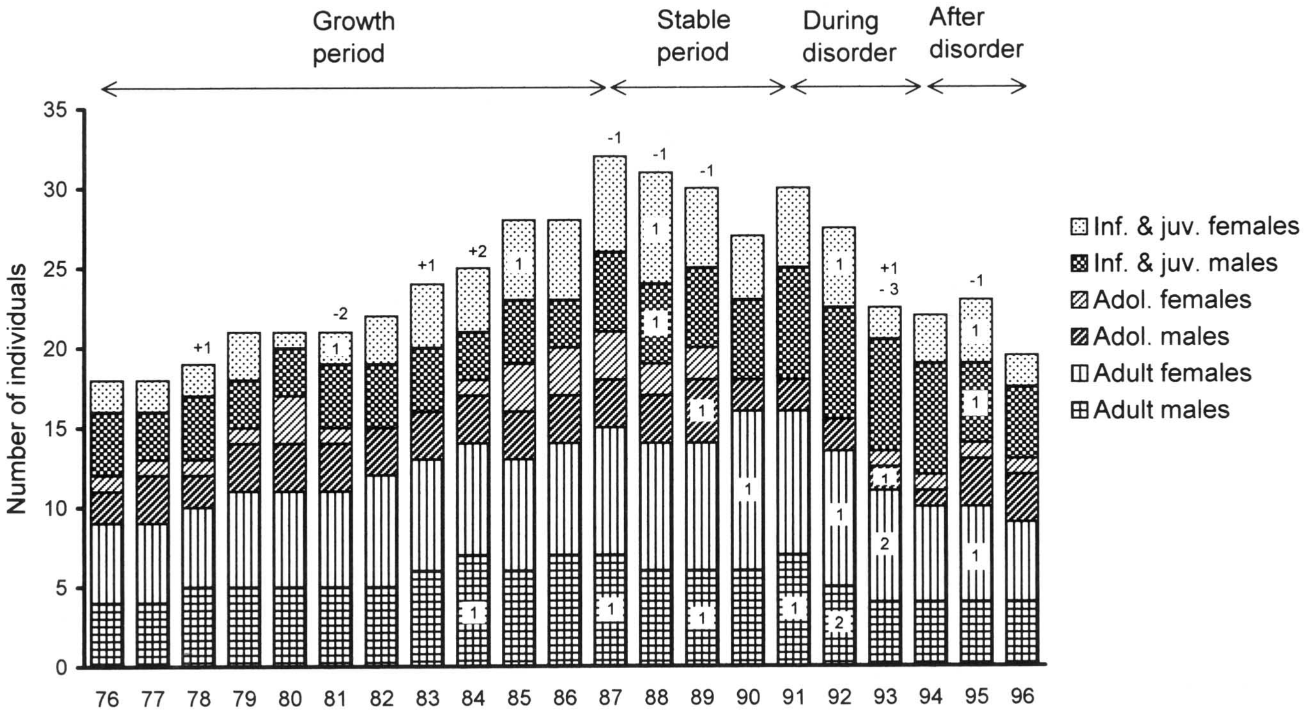

Fig. 1. Changes in size and composition of E1. Bars show numbers of individuals on January 1st of each year. Positive numbers above the bars indicate numbers of adolescent females that immigrated into the study group during that particular year. Negative numbers above the bars show numbers of juvenile or adolescent females that were assumed to have emigrated from the group. Numbers inside the bars show numbers of individuals of each age/sex class that we assume to have died.

Table I. Mortality of Different Age Classes in Different Study Periods[a]

	Growth period (Jan. 1976–Jan. 1987)	Stable period (Jan. 1987–Jan. 1991)	During disorder (Jan. 1991–Jan. 1994)	After disorder (Jan. 1994–Jan. 1996)	Overall mean	Overall mean except for during disorder
Infants and juveniles (≤7 years)[b]	0.027	0.056	0.033	0.094	0.040	0.041
Adolescent males (8–14 years old)	0.000	0.083	0.194	0.000	0.046	0.020
Adults (≥15 years)	0.006	0.050	0.144	0.050	0.040	0.022

[a] Values given are the mean yearly mortality during each period.

[b] Excluding females 7 years old.

during the stable period, -0.67 during the disorder, -0.50 after the disorder, and -0.20 over all periods. Only the growth period showed a positive rate, though it seems too small to explain the demographic development by itself.

Mortality During Different Periods

Number of deaths and yearly mortality of each age class in E1 are in Fig. 1 and Table I. Because females tend to leave their natal group at 7–9 years old (Furuichi, 1989; Idani, 1991; Kano, 1992), it was uncertain whether disappearing late juvenile and early adolescent females had died or emigrated. Therefore, we excluded data on 7-year-old females from the calculation of mortality of infants and juveniles, and calculated mortality of adolescents from data on males only.

Mortality of infants and juveniles was rather stable until 1994 and did not increase during the disorder. The high mortality value of infants and juveniles after the disorder is probably due to a small sample size. Adolescent mortality was very low in the growth period and after the disorder, and high during the disorder. For adults ≥ 15 years, mortality was very low during the growth period, and high during the disorder. Low mortality in all age classes seemed to be an important cause for demographic development during the growth period.

Averaging the data for all years from 1976 to 1996 gives similar mortality estimates for all age classes. If data from the disorder period are excluded, mortality estimates for adults and adolescents are lower than that for infants and juveniles.

Table II shows the survival ratio and mortality up to 6 years old. We constructed this figure using data for 22 individuals born in E1 from 1976 to 1990. Infant and juvenile survival was very high: 95.5 % survived to 1 year old and 72.7% survived to 6 years old. The score of yearly mortality is similar throughout the 6 years, though some fluctuation occurred due to the small sample size.

Table II. Mortality of Infants and Juveniles ≤6 Years Old

	Years from birth						
	0	1	2	3	4	5	6
Number of surviving individuals	22	21	20	19	18	18	16
Survival ratio	1.000	0.955	0.909	0.864	0.818	0.818	0.727
Yearly mortality		0.045	0.048	0.050	0.053	0.000	0.111

Table III. Birth Records of Females of E1 and E2[a]

Group	Female	1974	1975	1976	1977	1978	1979	1980	1981	1982	1983	1984	1985	1986	1987	1988	1989	1990	1991	1992	1993	1994	1995	1996
E1	Kame	o						o	x			o						d						
	Sen							o													d			
	Mitsu		o									o									d			
	Halu				o					o				o				o						
	Shiro					o				o						o				d				
	Bihi								o					o				o						o
	Mayu								o					o				o					d	
	Nao												ox		o						o			
	Miso													o				o		x	o			
	Kiku															o						o		
	Mean interbirth interval							4.8 years (n = 18)																
	Mean interval between live births							5.2 years (n = 15)																
E2	Fuji				o			o				o				o								
	Aki			o				o				o	x		o									
	Yasa					o						o												
	Suzu			o						o					o									
	Yuno				o						o					o	o							
	Bara											o			o									
	Mayuni									o						o								
	Mean interbirth interval							4.3 years (n = 14)																
	Mean interval between live births							4.4 years (n = 13)																
E1+E2	Mean interbirth interval							4.6 years (n = 32)																
	Mean interval between live births							4.8 years (n = 28)																

[a] o, birth; x, death of infant; d, death of the female. Birth records for E2 from 1990 are not shown because members of this group were not observed continuously. Two births in 1974 and 1975 were estimated from the size and behavior of the infants in 1976 (Kuroda, 1989; Hashimoto, 1997).

Interbirth Interval and Birth Rate

Table III shows births to females of E1 and E2. The mean interbirth interval is 4.8 years for E1, 4.3 for E2, and 4.6 for both groups. The mean interval between live births is 5.2 years for E1, 4.4 for E2, and 4.8 for both groups. Although E1 was subject to artificial provisioning more frequently than E2, there is no significant difference in interbirth interval between them. The interbirth interval and the interval between live births are slightly shorter than the value of 5 years given by Kano (1992).

Due to the short interbirth interval, some females were required to care for two dependent offspring at once. In 1991, two females in E1 frequently carried two nontwin offspring. That same year, two females in an almost unprovisioned neighboring group, P, each had two dependent offspring. The shortest documented interval between live births is 1 year, between 1988 and 1989 (Yuno, E2); the older offspring was frequently cared for by an adult male of the group.

For E1, the average number of births per year is 1.36 during the growth period, 1.75 during the stable period, 0.67 during the disorder, 0.50 after the disorder, and 1.25 over all periods. The average number of births per adult female per year is 0.21 during the growth period, 0.19 during the stable period, 0.10 during the disorder, 0.08 after the disorder, and 0.18 over all periods. Both the number of births per year and the number of births per female per year are higher during the growth and stable periods than during and after the disorder, but the differences are not statistically significant.

Monthly Distribution of Birth

We recorded 26 births in E1 during this study. Month of birth was confirmed by researchers for 11 births, by field assistants for 4 births, and was not confirmed due to the absence of observers for 11 births. Figure 2 illustrates the number of births in each month and shows the total number of observation days by researchers in each month, which may have influenced the probability of observation of birth.

Due to the small sample size and uneven distribution of observation days, seasonality of birth could not be tested statistically. However, birth frequency seemed relatively low from October to February, given the larger number of observation days. In contrast, births were frequently observed in March and April in spite of the smaller number of observation days. Births were also frequently observed by field assistants in April and May.

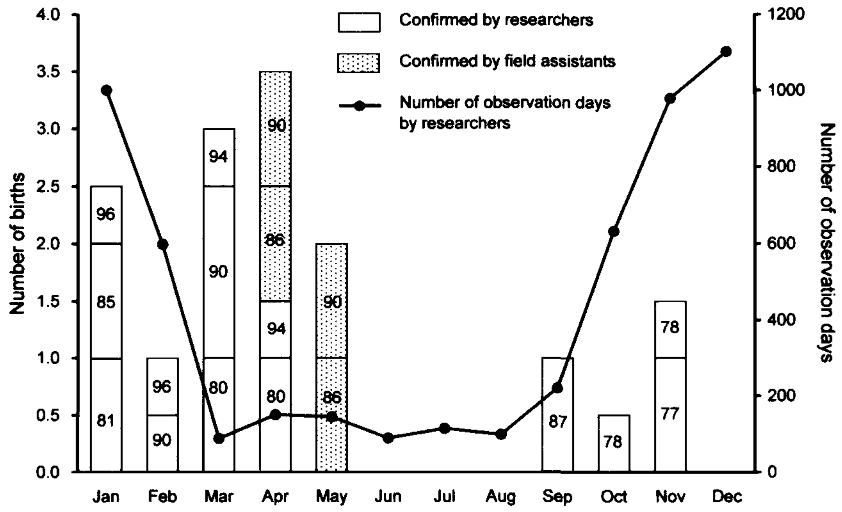

Fig. 2. Yearly distribution of births and total observation days. Bars show the number of individuals born in each month. Numbers in the bars show the year of each case of birth. For individuals whose estimated birthday spread over two months, we added 0.5 birth to each month. Number observation days indicate the accumulated number of observation days by all researchers since 1974 (Kano *et al.*, 1994).

DISCUSSION

The size of the study group increased between 1976 and 1987. The increase mainly seemed to be due to the low mortality in all age classes, but immigration of adolescent females from other groups might have contributed to the increase. Number of births per year and number of births per female per year during this period were not higher than in the succeeding stable period.

During the growth period, E split to E1 and E2, and their total home range expanded. Hashimoto *et al.* (1998) showed that the total and per capita home range area of E1 during the growth period was larger than in the later periods, which apparently facilitated an increase in group size. Alternatively, this increase might have been the result of artificial provisioning. Although there was no difference in the extent of provisioning between the growth period and subsequent stable period, it might have raised the carrying capacity to some extent.

Conversely, the size of the study group decreased from 1991 to 1994. The main cause for the decrease seemed to be high mortality in adults and adolescents. During this period, researchers were almost entirely absent from the study site, and some bonobos may have been killed by poachers.

Due to these changes in group size, the demographic variables may be of limited reliability. Nevertheless, we can provide important information on the demography of bonobos, because the study groups have been observed with identification of all members, for the longest period among wild bonobos.

Low Infant Mortality

One of the most conspicuous features of our results is the low mortality of immature individuals. At Gombe, 27.3% of chimpanzee babies died in the first year, and 15% of the remaining individuals died by the age of 5 years, giving a total of 38.2% mortality by the age of 5 years (Goodall, 1983). In chimpanzees of the Mahale Mountains, 53% of newborn babies died by the age of 6 years (Nishida *et al.*, 1990). In contrast, only 18.2% of Wamba bonobos died by age 5 years, and 27.3% died by age 6 years.

Very low mortality during the first and second year may be responsible for this low overall mortality of immature bonobos. In chimpanzees, mortality in the first year (Gombe) or in the first and second years (Mahale) was much higher than that in the succeeding years (Goodall, 1983; Nishida *et al.*, 1990). However, mortality of bonobos in these years was as low as in the succeeding years.

The difference in mortality during the first and second years may be due to differences in the nutritional condition of nursing mothers. Ecological factors, such as the abundance of fruits and herbaceous foods and the presence of large food patches (Kano and Mulavwa, 1984; White and Wrangham, 1988; Kano, 1992; Malenky *et al.*, 1994) are beneficial for females with nursing infants. The behavioral tendency for females to have priority of feeding in mixed parties (Furuichi, 1989, 1997; Kano, 1992; Parish, 1994) also aids lactating females.

Infanticide seems to be another cause of high mortality in the early stages of infancy in chimpanzees. At Gombe and Mahale, many chimpanzee infants were killed by adult members of the group (Goodall, 1977, 1986; Kawanaka, 1981; Nishida *et al.*, 1990). Most of them were killed in the first or second year after birth. In contrast, there is no record of infanticide in bonobos (Kano, 1992).

The low infant mortality may be partially biased by artificial provisioning. Even if the amount and duration of food provisioning were very limited, supplementary food during the dry seasons would be beneficial for mothers and infants. To evaluate the extent of this bias, we need to obtain more data from unprovisioned groups.

Seasonality of Birth

Our data suggest one birth peak per year, between March and May. This is the light rainy season, which falls just after the season with the least rainfall from December to February. At Wamba, availability of preferred fruit sources is greater during the rainy season (Kano and Mulavwa, 1984; Kano, 1992). This timing of birth seems optimal for infant survival because mothers will have the longest period after giving birth before they must face the dry season, when preferred food is least available.

The tendency in the timing of the birth peak seems to be common to bonobos and chimpanzees. Chimpanzees at Gombe show a birth peak in October, the last month of the dry season (Goodall, 1983). Chimpanzees at Mahale show two birth peaks per year, one of which occurs in the early rainy season (November to January), which falls just after the dry season (Nishida *et al.*, 1990). This tendency may also be similar to those of primates living at high latitudes. For example, *Macaca fuscata* gives birth just after the winter when food is least available (Takahata, 1980). Many studies on *Saguinus* spp. evidence a birth peak in spring, though the proximate cause for this might be photoperiod rather than food supply or the condition of mothers (McGrew and Webster, 1995).

Due to the small sample size and uneven monthly distribution of observations, we could not test the existence of a birth peak statistically. The assumption of an adaptive value of the birth peak in terms of food availability may be tested by analyses of monthly distribution of mortality of infants, which we did not do due to the small number of deaths.

Short Interbirth Interval

The interbirth interval of bonobos is shorter than that of chimpanzees. While the mean interval between live births of Wamba bonobos is 4.8 years, that for Gombe chimpanzees is 5.5 years (Goodall, 1986), and the median interval for Mahale chimpanzees is 6 years (Nishida *et al.*, 1990).

This difference may be due in part to habitat differences: Wamba bonobos inhabit a rain forest, while Gombe and Mahale chimpanzees inhabit much drier forests. The mean interbirth interval for chimpanzees in the Taï rain forest is 5.6 years, which is as long as those for chimpanzees in dryer forests. However, chimpanzees in the Bossou rain forest have an average of 5.1 years between live births, which number is reduced to 4.6 years if one extremely long interval of 11 years is excluded (Sugiyama, 1984, 1994). Further study of chimpanzees in rain forests and of bonobos in drier forests will clarify whether the short interbirth interval is a character unique to bonobos or if it is exhibited by both species living in rain forests.

Artificial provisioning of the main study group also may have biased our results by shortening the interbirth interval. However, comparative data from other Wamba groups show no evidence of bias. There is no statistically significant difference between the average interbirth intervals of E1 and E2, even though E2 was provisioned far less often. Furthermore, mothers carrying two dependent infants were observed not only in E1 but also in P, for which provisioning was negligible. These observations suggest that the interbirth interval of bonobos is fairly short even in unprovisioned groups.

The ecological and behavioral characteristics of bonobos, which favor nursing mothers, may also influence their mother–offspring relations. In addition to the shorter interbirth interval in bonobos, there are differences in mother-offspring interactions between bonobos and chimpanzees. Chimpanzees exhibit severe mother-offspring conflict during the weaning period (Clark, 1977; Tutin, 1979; Nishida, 1992). Mothers sometimes refuse suckling attempts and their offspring may interfere with the copulatory behavior of a mother that has resumed estrus. However, female bonobos carry and nurse two offspring if they give birth before weaning the older one, and offspring do not interfere with the mother's copulations (Hashimoto and Furuichi, 1994). The interbirth interval may be shortened, and mother–offspring conflict may be moderated, if mothers can afford to take care of more than one offspring.

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REFERENCES

Boesch, C. (1997). Evidence for dominant wild female chimpanzees investing more in sons. *Anim. Behav.* 54: 811-815.

Clark, C. B. (1977). A preliminary report on weaning among chimpanzees of the Gombe National Park, Tanzania. In Chevalier-Skolnikoff, S., and Poirier, F. E. (eds.), *Primate Bio-Social Development: Biological, Social and Ecological Determinants*, Garland, New York, pp. 235-260.

Furuichi, T. (1987). Sexual swelling, receptivity, and grouping of wild pygmy chimpanzee females at Wamba, Zaire. *Primates* 28: 309-318.

Furuichi, T. (1989). Social interactions and the life history of female *Pan paniscus* in Wamba, Zaire. *Int. J. Primatol.* 10: 173-197.

Furuichi, T. (1992). The prolonged estrus of females and factors influencing mating in a wild group of bonobos (*Pan paniscus*) in Wamba, Zaire. In Itoigawa, N., Sugiyama, Y., Sackett, G. P., and Thompson, R. K. R. (eds.), *Topics in Primatology, Vol. 2, Behavior, Ecology, and Conservation*, University of Tokyo Press, Tokyo, pp. 179-190.

Furuichi, T. (1997). Agonistic interactions and matrifocal dominance rank of wild bonobos (*Pan paniscus*) at Wamba, Zaire. *Int. J. Primatol.* 18: 855-875.

Goodall, J. (1977). Infant killing and cannibalism in free-living chimpanzees. *Folia Primatol.* 28:258-282.

Goodall, J. (1983). Population dynamics during a 15 year period in one community of free-living chimpanzees in the Gombe National Park, Tanzania. *Z. Tierpsychol.* 61: 1-60.

Goodall, J. (1986). *The Chimpanzees of Gombe: Patterns of Behavior*, Belknap, Cambridge.

Hashimoto, C. (1997). Context and development of sexual behavior of wild bonobos (*Pan paniscus*) at Wamba, Zaire. *Int. J. Primatol.* 18: 1-21.

Hashimoto, C., and Furuichi, T. (1994). Social role and development of noncopulatory sexual behavior of wild bonobos. In Wrangham, R. W., McGrew, W. C., de Waal, F. B. M., and Heltne, P. G. (eds.), *Chimpanzee Cultures*, Harvard University Press, Cambridge, MA, and London, pp. 155-168.

Hashimoto, C., Furuichi, T., and Takenaka, O. (1996). Matrilineal kin relationship and social behavior of wild bonobos (*Pan paniscus*): Sequencing the D-loop region of mitochondrial DNA. *Primates* 37: 305-318.

Hashimoto, C., Tashiro, Y., Kimura, D., Enomoto, T., Ingmanson, E. J., Idani, G., and Furuichi, T. (1998). Habitat use and ranging of wild bonobos (*Pan paniscus*) at Wamba. *Int. J. Primatol.* 19: 1045-1060.

Idani, G. (1991). Social relationship between immigrant and resident bonobo (*Pan paniscus*) females at Wamba. *Folia Primatol.* 57: 83-95.

Ihobe, H. (1992). Male-male relationships among wild bonobos (*Pan paniscus*) at Wamba, Republic of Zaire. *Primates* 33: 163-179.

Kano, T. (1982). The social group of pygmy chimpanzees (*Pan paniscus*) of Wamba. *Primates* 23: 171-188.

Kano, T. (1989). The sexual behavior of pygmy chimpanzees. In Heltne, P. G., and Marquardt, L. A. (eds.), *Understanding Chimpanzees*, Harvard University Press, Cambridge, MA, and London, pp. 176-183.

Kano, T. (1992). *The Last Ape: Pygmy Chimpanzee Behavior and Ecology*, Stanford University Press, Stanford, CA.

Kano, T., and Mulavwa, M. (1984). Feeding ecology of the pygmy chimpanzees (*Pan paniscus*) of Wamba. In Susman, R. L. (ed.), *The Pygmy Chimpanzee*, Plenum Press, New York, pp. 233-274.

Kano, T., Idani, G., and Hashimoto, C. (1994). The present situations of bonobos at Wamba, Zaire. *Primate Res.* 10: 191-214 (in Japanese with English abstract).

Kano, T., Bongoli, L, Idani, G., and Hashimoto, C. (1996). Challenge of Wamba. *Ethika Animali* 96: 68-74.

Kawanaka, K. (1981). Infanticide and cannibalism in chimpanzees, with special reference to the newly observed case in the Mahale Mountains. *Afr. Study Monogr.* 1: 69-99.

Kitamura, K. (1983). Pygmy chimpanzee association patterns in ranging. *Primates* 24: 1-12.

Kuroda, S. (1979). Grouping of the pygmy chimpanzees. *Primates* 20:161-183.

Kuroda, S. (1989). Developmental retardation and behavioral characteristics of pygmy chimpanzees. In Heltne, P. G., and Marquardt, L. A. (eds.), *Understanding Chimpanzees*, Harvard University Press, Cambridge, MA, and London, pp. 184-193.

Malenkey, R. K., Kuroda, S., Vineberg, E. O., and Wrangham, R. W. (1994). The significance of terrestrial herbaceous foods for bonobos, chimpanzees, and gorillas. In Wrangham, R. W., McGrew, W. C., de Waal, F. B. M., and Heltne, P. G. (eds.), *Chimpanzee Cultures*, Harvard University Press, Cambridge, MA, and London, pp. 59-75.

McGrew, W. C., and Webster, J. (1995). Birth seasonality in cotton-top tamarins (*Saguinus oedipus*) despite constant food supply and body weight. *Primates* 36: 241-248.

Nishida, T. (1992). Weaning conflict in chimpanzees. *Bull. Chicago Acad. of Sci.* 15: 14.

Nishida, T., Takasaki, H., and Takahata, Y. (1990). Demography and reproductive profiles. In Nishida, T. (ed.) , *The Chimpanzees of the Mahale Mountains: Sexual and Life History Strategies*, University of Tokyo Press, Tokyo, pp. 63-97.

Parish, A. R. (1994). Sex and food control in the "uncommon chimpanzee": how bonobo females overcome a phylogenetic legacy of male dominance. *Ethol. Sociobiol.* 15: 157-179.

Sugiyama, Y. (1984). Population dynamics of wild chimpanzees at Bossou, Guinea, between 1976 and 1983. *Primates* 25: 391-400.

Sugiyama, Y. (1994). Age-specific rate and lifetime reproductive success of chimpanzees at Bossou, Guinea. *Am. J. Primatol.* 32: 311-318.

Takahata, Y. (1980). The reproductive biology of a free-ranging troop of Japanese monkeys. *Primates* 21: 303-329.

Takahata, Y., Ihobe, H., and Idani, G. (1996). Comparing copulations of chimpanzees and bonobos: do females exhibit proceptivity or receptivity? In McGrew, W. C., Marchant, L. F., and Nishida, T. (eds.), *Great Ape Societies*, Cambridge University Press, Cambridge, pp. 146-155.

Tutin, C. E. G. (1979). Responses of chimpanzees to copulation, with special reference to interference by immature individuals. *Anim. Behav.* 27: 845-854.

Tutin, C. E. G. (1994). Reproductive success story. In Wrangham, R. W., McGrew, W. C., de Waal, F. B. M., and Heltne, P. G. (eds.), *Chimpanzee Cultures*, Harvard University Press, Cambridge, MA, and London, pp. 181-193.

White, F. J. and Wrangham, R. W. (1988). Feeding competition and patch size in the chimpanzee species *Pan paniscus* and *Pan troglodytes*. *Behaviour* 105: 148-164.

Wrangham, R. W. (1993). The evolution of sexuality in chimpanzees and bonobos. *Hum. Nature* 4: 47-79.