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Familial Incidence of Multiple Births in a Colony of Chimpanzees *(Pan troglodytes)*

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This paper describes the incidence of multiple births in the Yerkes Chimpanzee colony for a period of about 63 years. Pedigrees are presented for all multiple births. They demonstrate the recurrence of twins in relatively few family lines which can be traced back to a small number of ancestors. The findings suggest that twinning is a family trait in chimpanzees and they support the hypothesis that the incidence of multiple births is genetically influenced in this colony. In addition, a relatively high level of inbreeding may have enhanced the incidence of multiple births in these family lines. Similar findings are known from human populations.

Key words: Twinning · Inbreeding · *Pan troglodytes* · Chimpanzee

INTRODUCTION

Catarrhine primates usually give birth to single offspring, but multiple births may occasionally occur. The incidence of multiple births in catarrhine primates has recently been reviewed [11,12], showing that the frequency of twinning can be estimated with reasonable reliability for only a few species of Old World monkeys. In these species, the twinning frequencies appear to be lower than those of most human populations.

Repeated births of twins with the same father, with the same mother or with related parents have been reported for a few colonies of Old World monkeys [1,4,22], whereas in the remaining colonies all twins were from different family lines [24, see also 12].

In three chimpanzee colonies, a conspicious recurrence of multiple births has been reported [11-14,16, 21]. A detailed analysis of these data has

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not yet been provided. The most promising data set, on grounds of sample size, is that of the Yerkes Chimpanzee colony. The most recent census from 1981 reports that 304 births had been recorded at the colony between 1930 and 1979 [16]. These births were delivered by 72 chimpanzee mothers and sired by 27 males. The same census mentions 12 multiple births, 8 sired by one male and 5 delivered by one female [16]; but additional twin births have occurred since then (see below). This paper describes the incidence of multiple births in the Yerkes Chimpanzee colony over a period of about 63 years.

MATERIAL AND METHODS

Data presented in this study were extracted from the records of the Yerkes Regional Primate Research Center. These records have been kept since the colony's origin and in most cases permit reconstruction of accurate pedigrees for each animal, with only a few cases of unknown or uncertain paternity. This study encompasses all known incidences of multiple births in the colony for the period from the beginning of formal record-keeping in 1925 until August 9, 1988.

Males are symbolized by squares in the pedigree charts illustrated below, and have identification numbers ending in odd integers, while females are symbolized by circles in the pedigree charts and have identification numbers ending in even integers. The identification numbers are those used at the Yerkes Primate Center.

In this study, the term "ancestor" is used for every individual from which another one is descended, whether on the father's or mother's side, at any distance of time.

Inbreeding coefficients (F_0 = the probability that two genes at any locus in an individual are identical by descent) were calculated according to the method of Kudô [15].

RESULTS

In a previous report on the breeding history of the Yerkes Chimpanzee colony [16], 304 births had been reported for the time up to December 1979. Between 1980 and July 16, 1988, 84 additional births had occurred. On May 10, 1988, the colony comprised 171 chimpanzees (Ms. G. Cannon, personal communication).

During a period of about 63 years, 17 multiple births have been recorded

at the colony (Table I). Most were twin births; only one triple birth has been recorded in this colony, not two, as indicated in a figure of a recent study [6].

Pedigree charts for all 17 multiple births are illustrated in Figure 1. They show a striking recurrence of some individuals as parents or ancestors of multiple offspring. All parents of more than one multiple birth are listed in Table II. Of the 21 parents of multiple offspring, four (19.0%) gave birth to more than one set. The most prolific male (Hal, C0043) sired 8 (47.1%) of the 17 sets of multiple offspring. The most prolific female (Flora, C0100) gave birth to five (29.4%) sets, not 6 sets, as stated in an earlier study [16, p. 345]. Two female twins (Helene, C0062, and Martha, C0204) gave birth to twins themselves.

Table III lists the individuals which are ancestors of more than one multiple birth. "Direct ancestors" (= parents) of multiple offspring are not included in this table. Most multiple births can be traced back to only a few individuals. One male (Jack, C0017) is ancestor of 13 of 17 multiple births (76.5%), two other males and one female are ancestors to nine multiple births each (52.9%). One of these males (Pan, C0003) is also father of an additional set of multiple offspring.

For most sets of multiple births, the pedigree charts show no evidence of inbreeding, but three (17.6%) do: an inbreeding coefficient of 0.125 has been calculated for two of these sets (Figure 1b); for the third set (Figure 1h), the coefficient is lower: 0.0078. The mean inbreeding coefficient for all multiple births of the colony is 0.0152.

DISCUSSION

It is generally believed that genetic factors influence the occurrence of twinning in human populations, although the details remain unclear. Pedigree studies have confirmed that twinning is a family trait in human beings (the evidence on the inheritance of twinning in man has been reviewed [2,8]). Genetic mechanisms operating in the etiology of twinning have also been suggested for some strepsirhine primates, such as *Lemur catta* and two taxa (probably two distinct species [5]) of *Galago* [18,19,23], but apparently not for any catarrhine primate other than humans.

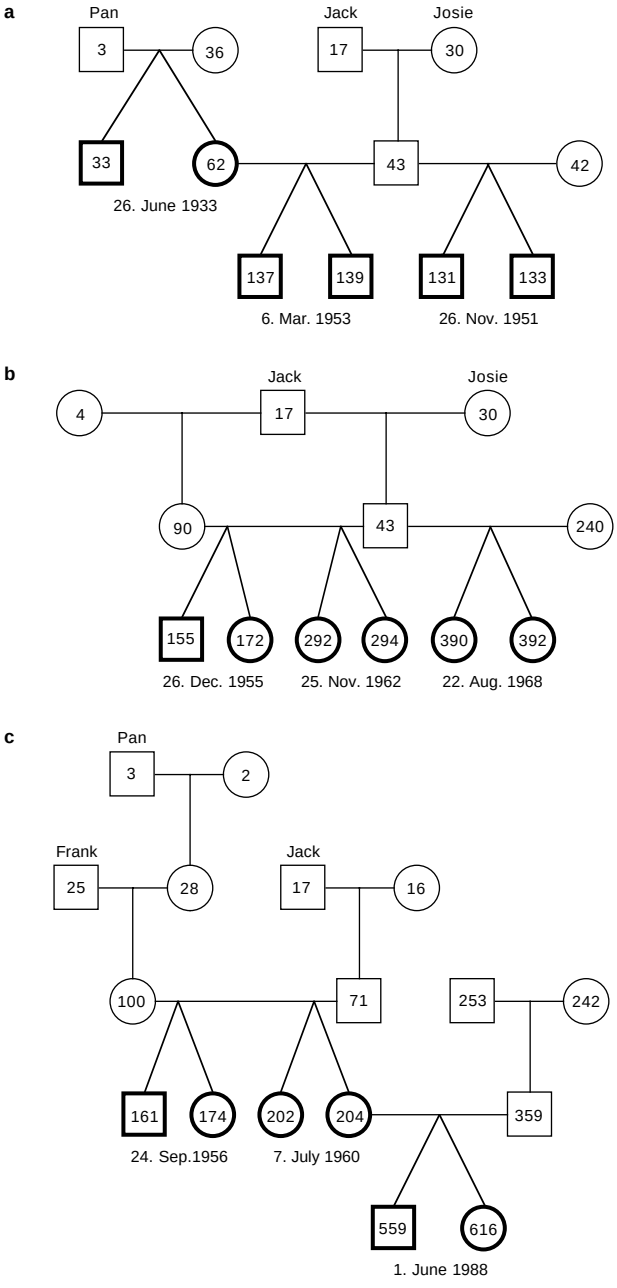
This study demonstrates an accumulation of multiple births, which does not seem to be fortuitous, within a chimpanzee colony. A concentration of multiple offspring born to relatively few parental animals in this colony has been mentioned previously [11-14,16,21], and these findings have been confirmed by the present investigation. However, neither an individual pro-

TABLE I. Multiple births in the Yerkes Chimpanzee colony

Date of birth	Father	Mother	Multiple off-spring	Sex	Date of death and comments
26. Jun 1933	C0003 Pan	C0036 Mona	C0033 Tom	M	Died 14 Aug 1948
			C0062 Helene	F	Traded 20 Jan 1970
26. Nov 1951	C0043 Hal	C0042 Pati	C0131	M	Stillborn
			C0133	M	Stillborn
6. Jun 1953	C0043 Hal	C0062 Helene	C0137 Neut	M	Died 10 Jun 1953
			C0139 Alec	M	Died 27 Sept 1962
26. Dec 1955	C0043 Hal	C0090 Jenny	C0155	M	Died 28 Dec 1955
			C0172	F	Probably stillborn
24. Sept 1956	C0071 Jent	C0100 Flora	C0161	M	Died 27 Sept 1956
			C0174	F	Died 27 Sept 1956
21. May 1957	C0105 Ked	C0102 Fanny	C0167 Klem	M	Died 28 Sept 1962
			C0180	F	Died 23 May 1957
7. Jul 1960	C0071 Jent	C0100 Flora	C0202 Mary	F	Still alive on 9 Aug 1988
			C0204 Martha	F	Still alive on 9 Aug 1988
25. Nov 1962	C0043 Hal	C0090 Jenny	C0292	F	Found dead after premature birth (gestation: 226 days)
			C0294	F	Found dead after premature birth (gestation: 226 days)
5. Jul 1967	C0043 Hal	C0100 Flora	C0376	F	Lived 4 hours, weight 550g
			C0378	F	Lived 4 hours, weight 520g
			C0289	M	Stillborn, weight 635g

TABLE I. (ctd.)

Date of birth	Father	Mother	Multiple off-spring	Sex	Date of death and comments
22. Aug 1968	C0043 Hal	C0240 Banana	C0390	F	Stillborn
			C0392	F	Stillborn
9. Dec 1969	C0043 Hal	C0100 Flora	C0319 Richard	M	Traded 1 Jul 1980
			C0321	M	Stillborn
17. May 1972	C0043 Hal	C0100 Flora	C0446 Mickie	F	Weight 1280g, C-section, handreared, still alive on 9 Aug 1988
			C0448 Joice	F	Weight 1590g, C-section, handreared, still alive on 9 Aug 1988
3. Aug 1984	C0389 Rogger	C0488 Lil'One	C0509 Lyons	M	Handreared, still alive on 9 Aug 1988
			C0511 Hunter	M	Handreared, still alive on 9 Aug 1988
18. Sept 1984	C0409 Walnut	C0506 Gwennie	C0515 Mason	M	Weight 650g, C-section, handreared, still live on 9 Aug 1988
			C0517 Dixon	M	Premat. birth, C-section, died 22 Sept 1984
1. Aug 1986	C0295 Duncan	C0382 Foxy	C0529 Justin	M	Handreared, still alive on 9 Aug 1988
			C0531	M	Stillborn, C-section.
1. Jun 1988	C0359 Chuck	C0204 Martha	C0559	M	Stillborn. Product of artif. insemination.
			C0616 Kengee	F	Product of artif. insemination, still alive on 9 Aug 1988
2. Jun 1988	C0369 Boisfeuillet	C0200 Boka	C0618	F	Stillborn
			C0620	F	Stillborn


a
Pan
3
36
Jack
17
Josie
30
33
62
43
42
26. June 1933
137
139
131
133
6. Mar. 1953
26. Nov. 1951
b
Jack
Josie
4
17
30
90
43
240
155
172
292
294
390
392
26. Dec. 1955
25. Nov. 1962
22. Aug. 1968
c
Pan
3
2
Frank
25
28
Jack
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24. Sep.1956
7. July 1960
559
616
1. June 1988

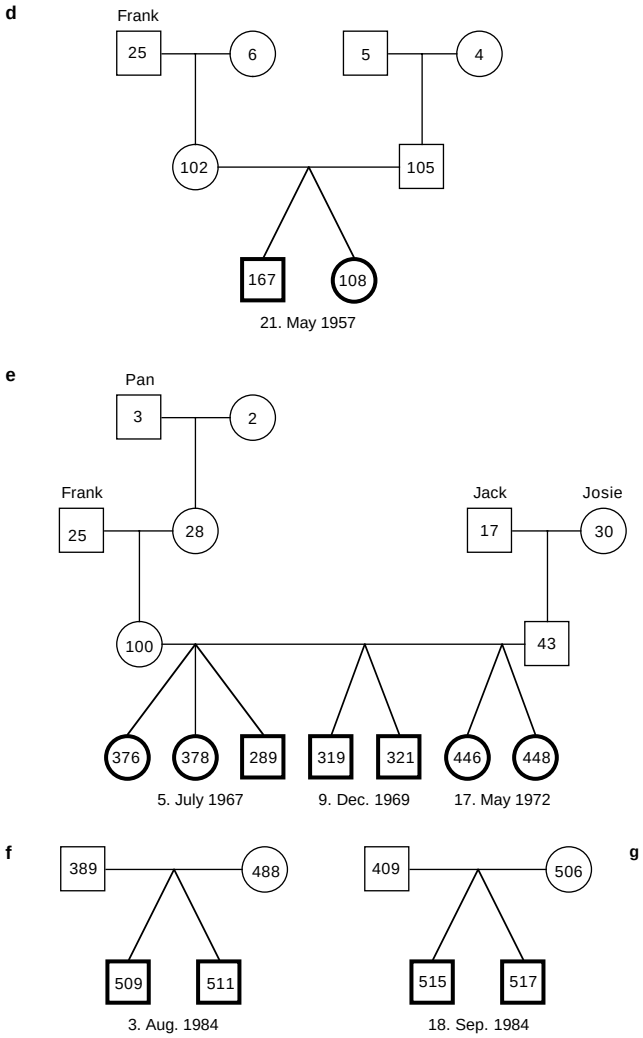

Fig. 1a-i. Pedigree charts of all multiple births at the Yerkes Chimpanzee colony over the period covered by this study. Only family lines ending in multiple offspring are shown. Symbols for twins are highlightened by heavy frames. Individual names indicate ancestors of more than 50% of the colony's multiple births. Figure continues nest page.

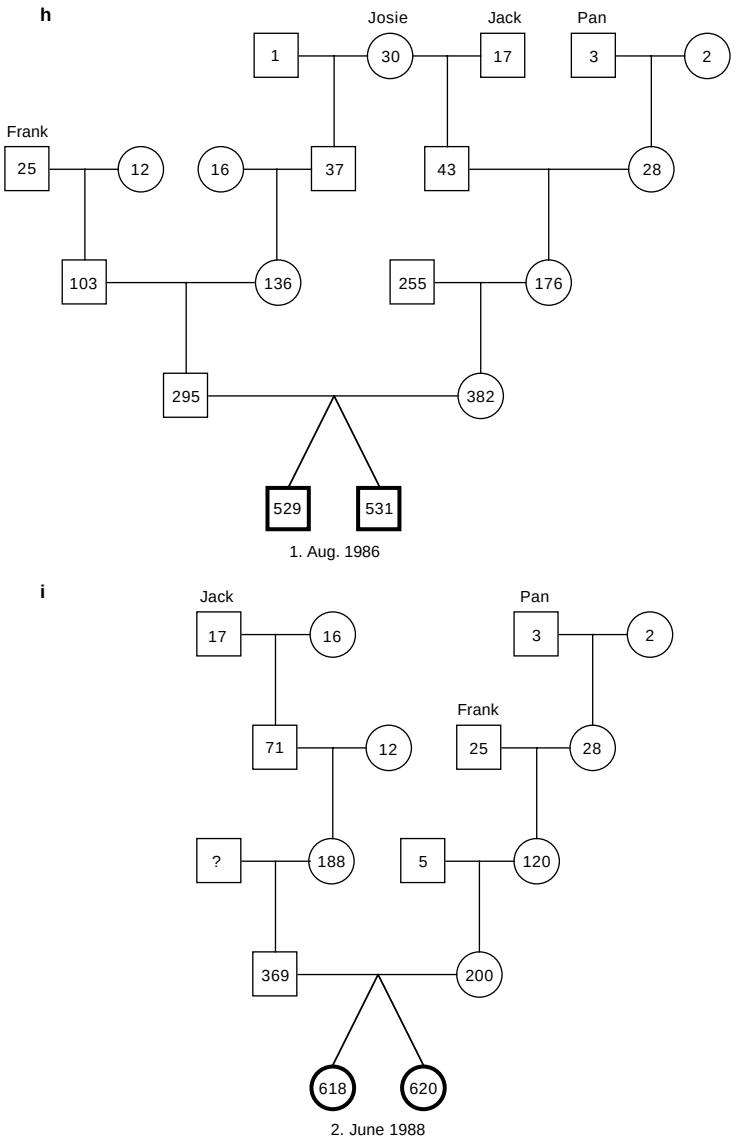

Fig. 1h,i. Continued from previous page.

TABLE II. Parents of more than one multiple birth

Parent	ID No.	Number of multiple births	% of total number of multiple births (17)
Hal	C0043	8	47.1
Flora	C0100	5	29.4
Jenny	C0090	2	11.8
Jent	C0071	2	11.8

TABLE III. Ancestors (but not parents) of more than one multiple birth

Parent	ID No.	Number of multiple births	% of total number of multiple births (17)
Jack	C0017	13	76.5
Pan	C0003	9	52.9
Frank	C0025	9	52.9
Josie	C0030	9	52.9
Dwina	C0002	8	47.1
Bentia	C0016	5	29.4
Wendi	C0004	3	17.6
Soda	C0012	2	11.8
Bokar	C0005	2	11.8

pensity for multiple births nor the recurrence of multiple births to related animals is necessarily genetic in origin [12,17]. Non-genetic factors (environmental causes) could also account for these observations.

The observations presented in this study provide a more detailed picture: (1) only a few males and a few females in the chimpanzee colony produce multiple offspring, (2) some males and some females have produced more than one set of multiple offspring, (3) only a few males and a few females are ancestors of twins, (4) female twins themselves produce twins. These observations suggest that the incidence of multiple births is a family trait in the Yerkes Chimpanzee colony and support the hypothesis that the incidence of multiple births is genetically influenced in this colony.

If a propensity toward twinning is inherited, the presence of twin-prone animals in populations with a high amount of inbreeding may lead to unusually high twinning frequencies. This effect has in fact been suggested to account for the elevated twinning frequencies recorded in extremely endogamous and isolated human populations in the Åland Islands [7-10].

Elevated twinning frequencies have also been recorded in other relatively isolated and endogamous human populations [3,20].

It has been suggested that the twinning frequency in the Yerkes Chimpanzee colony may be biased due to the presence of twin-prone animals and possibly a high degree of inbreeding [11,12,21]. In fact, a recent study on this colony, covering the time period from 1925 to 1976, found the inbreeding in this colony to be "distributed in a strikingly nonrandom manner" [6]. Evidence for inbreeding was found for only 20 out of 264 sibships (7.6%). This percentage was thought to be relatively low because of frequent additions of animals to the colony. The mean inbreeding coefficient of the whole colony was 0.0045; the mean inbreeding coefficient for all chimpanzees born in the colony was 0.0079, and the highest inbreeding coefficient for any individual was 0.125. This highest coefficient was also found with some individuals that were not twins (judging from Figure 2 in [6]).

The inbreeding coefficient of the small sample of family lines with multiple births presented in this study cannot be statistically compared with the inbreeding coefficients found for all animals of the colony [6]. Nevertheless, the inbreeding coefficients found for the multiple births seem, as a trend, to be somewhat higher: Evidence for inbreeding was found for 3 out of 17 multiple births (17.6%). Over the period encompassed by this investigation (1925-1988), the mean inbreeding coefficient for all multiple births is 0.0152. If only the births occurring between 1925-1976 are considered, as in the study on all animals of the colony [see 6], 12 multiple births remain, and their mean inbreeding coefficient is even higher: 0.0208. The highest inbreeding coefficient for any multiple birth is 0.125, identical to the highest inbreeding coefficient found for any non-twin. This trend is at least consistent with the hypothesis that a relatively high level of inbreeding may have enhanced the incidence of multiple births in the respective family lines.

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