

**multiple
births
in catarrhine
monkeys
and apes**

A Review

by
**THOMAS
GEISSMANN**



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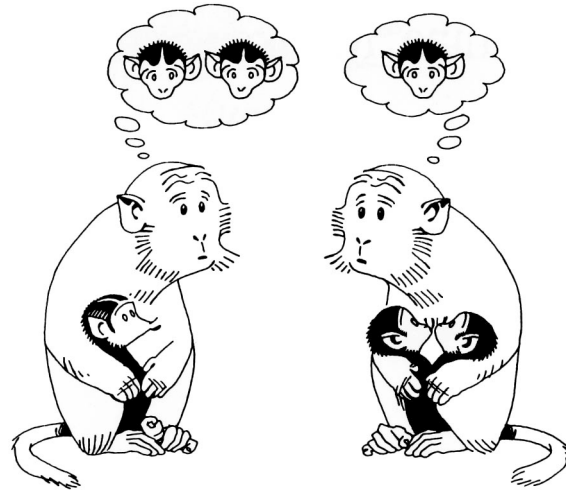
Thomas Geissmann

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Catarrhine Monkeys and Apes

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Cover:

A female crab-eating macaque (*Macaca fascicularis*) with her twin offspring, based on a photograph taken by J. Hess-Haerer in ANONYMOUS (1970).

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«Such is the nature of a monkey that, when she gives birth to twins, she esteems one of them highly but scorns the other. Hence, if it ever happens that she gets chased by a sportsman she clasps the one she likes in her arms in front of her, and carries the one she detests with its arms round her neck, pickaback. But for this very reason, when she is exhausted by running on her hind legs, she has to throw away the one she loves, and carries the one she hates, willy-nilly.»

(Anonymous, from a Latin bestiary of the twelfth century, translated by T.H. WHITE, 1960, p. 34).

Introduction

Multiple births occur with varying frequency in primates (e.g. SCHULTZ, 1956; WILDT & DUKELOW, 1974). Catarrhine primates (Old World monkeys and apes) are considered to be monovulatory species here, single births are the rule (e.g. HENNRICKX & NELSON, 1971; SCHULTZ, 1972). It is known that multiple births do occasionally occur in various catarrhine species. However, the distribution of the phenomenon and the frequency of its occurrence are still unknown. It has been suggested that multiple births may occur in many, if not all Old World monkeys and apes (HARMS, 1956; SCHULTZ, 1948; YERKES, 1934).

SCHULTZ (1948) listed the known cases of multiple births in nonhuman catarrhine species and presented – subsequent only to the study of ABEL (1933) – one of the earliest attempts at quantifying the incidence of plural births in these primates. Since then, supplementary information on this topic has been compiled in several articles (e.g. BENIRSCHKE, 1986; HARMS, 1956; HENDRICKX & NELSON, 1971; SCHULTZ, 1956, 1972; WILDT & DUKELOW, 1974), but, following SCHULTZ's (1948) report, no attempt has apparently been made to comprehensively gather the widely distributed published accounts on multiple births.

In the present report, the pertinent literature on multiple births in catarrhine monkeys and apes is reviewed. The principal aims of this review are: (1) to compile the available evidence, (2) to survey the numerous short reports which make up most of the relevant literature, and (3) to assess current hypotheses regarding occurrence, causes and consequences of multiple births in nonhuman catarrhine primates. This undertaking is of potential medical interest, as these simians have been proposed as models for comparative studies on multiple births in man (WILDT & DUKELOW, 1974, see also PASZTOR & VAN HORN, 1979). «A model for human twinning would be advantageous in studies of the genetic expression of this characteristic or in certain physiological research problems such as maternal nutritive support of twins vs. singletons.» (WILDT & DUKELOW, 1974, p. 15). In addition, the occurrence of twin births may influence reproductive success in primate breeding colonies. As treatment with gonadotropins for induction of ovulation has been found to result frequently in multiple pregnancies, the possibility has even been raised that treated macaque colony females could in future furnish litters of three or more infants (VAN WAGENEN, 1968a).

Material and methods

This report covers the major topics which emerged from a review of the pertinent literature on multiple births in nonhuman catarrhine primates.

The survey is not intended to be exhaustive and additional information is doubtless to be found, particularly in reports from zoological gardens. In addition to information already published, new data on the incidence of multiple births were collected during a short stay at the Yerkes Regional Primate Research Center, Atlanta. A detailed report on the results of this investigation will be published elsewhere (GEISSMANN, 1990), but some preliminary results are included in this review.

Chapter 8 on twinning frequency has been published previously as a separate article (GEISSMANN, 1989). It has been slightly expanded for inclusion in this monograph.

Throughout this paper, the terms 'Catarrhini' and 'Hominoidea' will both be used to the exclusion of humans. For brevity the adjective 'nonhuman' will not be mentioned each time.

Nonparametric statistical tests (two-tailed) are adapted from SIEGEL (1959). Parametric tests follow CAYALLI-SFORZA (1980); for the significance thresholds of the F- and the Chi-square-distribution the tables of CIBA-GEIGY (1980) are used.

Occurrence of multiple births in various catarrhine species

The earliest description of an authentic case of twinning was apparently provided by SELENKA (1892) for *Macaca fascicularis*. SCHULTZ (1948) listed as many as 16 cases of multiple births in 10 nonhuman catarrhine species. This survey covers reports on 178 cases of multiple births, from representatives of 28 species. In *Table 1*, the numbers of reported cases for each species are listed along with the respective sources. Supplementary publications containing additional information on already published cases are also included in the list. If it could not be definitely decided whether two articles concerned the same set of twins or not, the set in question was counted only once.

Vague published statements such as: ‘females of species *x* may occasionally’ or ‘not unfrequently have two young at a birth’ (see e.g. PHILLIPS, 1935, for *Macaca sinica*, *Presbytis vetulus* [= *senex*], and *P. entellus*, and BLANFORD, 1888-91, for *P. entellus*), or «Twin births seem to occur more frequently in *Presbytis entellus schistaceus*» (OBOUSSIER & V. MAYDELL, 1960, p. 145) were ignored.

Several instances of possible cases of twins which were labelled by the authors as doubtful have also been excluded. They may be briefly summarized as follows:

- one case in captive hamadryas baboons (KNOTTNERUS-MEYER, 1909);
- one case in wild-shot black-and-white colobus monkeys (VOSSELER, cited by HECK, 1916, p. 599)
- two cases in gorillas: one in captivity (KRUMBIEGEL, 1954, p. 343f), and one from a wild-shot female (FLEISCHHACKER, 1968; KIRCHSHOFER *et al.*, 1968);
- one of two cases in feral chimpanzees (GOODALL, 1983, 1986).

Doubts on the authenticity of captive twins arose mainly in certain earlier reports, as infant monkeys or apes of similar age seem to have been exhibited quite frequently as twins, obviously in order to enhance the public’s interest (HARTMAN, 1938; KNOTTNERUS-MEYER, 1909; YERKES, 1934).

Aunting, adoption and kidnapping behaviors have been observed to occur in several primate species, in both captive and feral animals (see e.g. DEETS & HARLOW, 1974; HRDY, 1976, 1977; JOLLY, 1972; QUIATT, 1979; THIERRY & ANDERSON, 1986). This can also result in a female carrying two infants, «pseudo-twins» (ASANOV & LIPPERT, 1976; DOLHINOW, 1980; JAY, 1965; KOFORD *et al.*, 1966; LAPIN & YAKOVLEVA, 1963; ROSENBLUM, 1968) which can be mistaken for real twins (HARTMAN, 1938). If the previous individual history of the animals is not known and the birth was not observed (as is very

TABLE 1 – *Multiple births in nonhuman catarrhine primates, as compiled from a survey of the literature.*

Species	References	Number of cases	Remarks
<i>MACACA</i>			
<i>arctoides</i>	BRÜGGEMANN & GRAUWILER, 1972 CHRISTIE, 1969 HENDRICKX & NELSON, 1971 SCHRIER & POVAR, 1984	4	
<i>fascicularis</i>	ANONYMOUS, 1970 ANONYMOUS, 1982 Bolk, 1926 HARMS, 1956 Hein <i>et al.</i> , 1985 RUDAT, 1948 SCHULTZ, 1956 SELENKA, 1892 THOMMEN, 1981	8	1 double monster
<i>fuscata</i>	ITANI, 1959 MATSUI, 1979, cited in NAKAMICHI, 1983 NAKAMICHI, 1983 TANAKA <i>et al.</i> , 1970	4	
<i>mulatta</i>	ANONYMOUS, 1979 ASANOW & LIPPERT, 1976 COURTNEY & VALERIO, 1968 DEETS & HARLOW, 1974 GAREY <i>et al.</i> , 1985 HARTMAN, 1943 HENDRICKX & NELSON, 1971 HINDE, 1969, 1972 KOFORD <i>et al.</i> , 1966 LAPIN & YAKOVLEVA, 1963 MAHONEY <i>et al.</i> , 1979 NESTURKH, 1959 PASZTOR & VAN HORN, 1976, 1979 RAWLINS & KESSLER, 1986 RAWLINS <i>et al.</i> , 1984 SCHRIER & POVAR, 1984 SCHULTZ, 1948 SPENCER-BOOTH, 1968 TAUB, 1983 VALERIO <i>et al.</i> , 1969 VAN WAGENEN, 1968a, 1972 VAN WAGENEN & ASLING, 1964	33	1 double monster
<i>nigra</i>	BREITINGER, 1951	1	1 triple birth
<i>radiata</i>	HENDRICKX & NELSON, 1971 RAHAMAN & PARTHASARATHY, 1969	3	
<i>sinica x radiata</i>	HAMERTON, 1937		
<i>sylvanus</i>	BURTON & DE PELHAM, 1979 BURTON & SAWCHUK, 1974 PAUL & THOMMEN, 1984a, b SCHAUB, 1987	8	

(continued)

TABLE 1 (continued)

Species	References	Number of cases	Remarks
<i>CERCOCEBUS</i>			
<i>torquatus</i>	HENDRICKX & NELSON, 1971		
<i>PAPIO</i>			
<i>anubis</i>	HENDRICKX <i>et al.</i> , 1968, 1971 HILL, 1970 SCHULTZ, 1948	5	
<i>hamadryas</i>	ABEL 1932, 1933 ASANOW & LIPPERT, 1976 BREITINGER, 1951 BUNGARTZ, 1949 EIFFERT, 1951 HECK, 1916 HEDIGER & ZWEIFEL, 1962 KNOTTNERUS-MEYER, 1909 LAPIN & YAKOVLEVA, 1963 NESTURKH, 1939 NOGGE, 1981, 1982, 1983 RUDAT, 1948	15	
<i>papio</i>	RAFERT & VOJIK, 1983	1	
<i>ursinus</i>	FITZSIMONS, 1919 PIENAAR, 1964	3	
<i>THEROPITHECUS</i>			
<i>gelada</i>	ANONYMOUS, 1968	1	
<i>P. hamadryas x T. gelada</i>	ASANOW & LIPPERT, 1976	2	
<i>MANDRILLUS</i>			
<i>sphinx</i>	CRANDALL, 1964 FIEDLER <i>et al.</i> , 1968 HILL, 1970 LITTLEWOOD & SMITH, 1979 WITSTRUK, 1985	6	
<i>CERCOPITHECUS</i>			
<i>albogularis</i>	WISLOCKI, 1939	1	
<i>pygerythrus</i>	FITZSIMONS, 1919	2	
<i>sabaeus</i>	ANONYMOUS, 1932 STOTT, 1946	1	
<i>ERYTHROCEBUS</i>			
<i>patas</i>	ASANOW & LIPPERT, 1976 SLY <i>et al.</i> , 1983	3	
<i>COLOBUS</i>			
<i>guereza uellensis</i>	CRANDALL, 1964	1	
<i>PRESBYTIS</i>			
<i>entellus</i>	HRDY, 1976, 1977 MOHNOT & MOHNOT, 1982 SAPKAL, 1984	8	
<i>melalophos</i>	BENNETT, 1982, 1988	1	
<i>NASALIS</i>			
<i>larvatus</i>	SCHULTZ, 1942 WISLOCKI, 1939	1	
Total for Cercopithecoidea		116	

(continued)

TABLE 1 (continued)

Species	References	Number of cases	Remarks
<i>HYLOBATES</i>			
<i>lar</i>	ELLEFSON, 1974 MOOTNICK, 1984 SWIGERT, 1983	5	
<i>syndactylus</i>	SCHMIDT, in press SULAK, 1984 YOUNG, 1984, 1985	5	
<i>PONGO</i>			
<i>pygmaeus</i>	ANONYMOUS, 1977, 1978a, b, c, d BOND & BLOCK, 1982 HEINRICHS & DILLINGHAM, 1970 JONES, 1982 KRUMBIEGEL, 1954 LANG, 1975 NELSON, 1974 OLSEN, 1976 OMAR, cited in BENNETT, 1988 SAVAGE, 1982 SAVAGE & SNOWDON, 1982 YELVERTON, 1974	11	
<i>GORILLA</i>			
<i>gorilla</i>	ANONYMOUS, 1981 FLEISCHACKER, 1968 GRZIMEK <i>et al.</i> , 1968 HANNA & JULY, 1985 KIRCHSHOFER <i>et al.</i> , 1968 MURPHY, 1982 ROSEN, 1972 SABATER-PI, 1982 WATTS & HESS, 1988 YERKES PRIMATE CENTER, RECORDS (1981), unpubl.	6	
<i>PAN</i>			
<i>trogodytes</i>	ANONYMOUS, 1972 BOURNE, 1967 BOURNE <i>et al.</i> , 1975 BREITINGER, 1951 BÜTZER & JEKER, 1981, p. 90 GEISSMANN, 1990 GEWALT & MASSELER, 1977 GOODALL, 1979, 1983, 1986 GUILLOUD, 1969 HEDIGER & ZWEIFEL, 1962 KASZA, 1977 MARTIN, 1981 MAUERHOFER, 1983 NESTURKH, 1959 NISSEN & YERKES, 1945 PEACOCK & ROGERS, 1959 ROBINSON, 1987 ROSENTHAL, 1981 SCHULTZ, 1948 SEAL <i>et al.</i> , 1985 SHTEFKO, 1940 SHTEFKO & KHAR'KOV, 1946 TOMILIN & YERKES, 1935 TSVETAYEVA, 1941, cited in LAPIN & YAKOVLEVA, 1965 YAMAMOTO, 1967 YERKES, 1954, 1943	37	3 triple births
Total for Hominoidea		62	

often the case in free-ranging primates), twins often cannot be recognized as such with certainty (GOODALL, 1983, 1986; KRISHNAN, 1971, p. 540; YERKES, 1934).

Also excluded from comparison was a presumed case of superfetation in a patas monkey (*Erythrocebus patas*): a female gave birth to two «full term» young within an interval of three months (LEAKEY, 1969).

The distribution of twinning throughout the various species supports the observation by SCHULTZ (1948) that twins among monkeys and apes seem to be found particularly in species which are especially numerous both in the wild and in captivity and which breed most readily in collections, i.e., macaques (*Macaca mulatta*), baboons (*Papio hamadryas*), and chimpanzees (*Pan troglodytes*). It is therefore quite probable that, as more births are recorded, twinning will be found to occur in a wider variety of species.

Triple births

Only four cases of triple births have been reported for nonhuman catarrhine primates. When «for the first time in history birth of triplets in a mookey» (*Macaca mulatta*) was reported in the New York press, HARTMAN (1938) reviewed the evidence and concluded «that the case was not one of multiple birth but one of multiple kidnapping». However, since the same female delivered a double-headed monster one year later, HARTMAN (1943) subsequently wondered «if the mother should not perhaps be credited at least with twins (though not with triplets)».

Apparently, only one case of a triple birth in an Old World monkey has been reliably recorded: In 1945, a black Celebes macaque (*Macaca nigra*) gave birth to triplets. All infants were stillborn and the mother died from exhaustion (BREITINGER, 1951).

The only other cases of triplets (3 sets) have all been reported for the chimpanzee:

– The first set of triplets was reported from the Yerkes Laboratories, Florida (BOURNE, 1967) and was born in 1967. One of the prematurely born infants (the male) was stillborn, the other two (females) soon died, one during the first day, the other on the second day after birth. The body weights of the three infants ranged between 520 and 635 g.

– A second record of a chimpanzee triple birth was provided by KASZA (1977). The triplets, born 1976 in the Veszprém Zoological Garden, were found dead. They were very small, the weight of one of the newborn being merely 280g. The average chimpanzee birth weight has been reported to range between 1.5 and 2 kg (KEELING & ROBERTS, 1972).

– Another female chimpanzee gave birth to a set of triplets at the Lincoln Park Zoological Gardens, Chicago in 1979 (ROSENTHAL, 1981). Two of the three male infants were dead when they were discovered, the third male died on the seventh day.

Although the frequency of triple births in the total of multiple births (see *Table 1*) seems to be somewhat lower in Old World monkeys (0.9% or 1 in 116) than in apes (4.8% or 3 in 62), the difference is not statistically significant (Fisher exact probability test, $p = 0.23$). A comparison between chimpanzees and non-chimpanzees approaches significance (Fisher exact probability test, $p = 0.057$).

Of the four recorded sets of triplets, most infants were stillborn; none survived longer than 7 days.

Zygoty of twin sets

The type of twinning is known chiefly for those sets of twins consisting of a male and a female, which are clearly dizygotic. Such is the case in 17 out of 52 sets for cercopithecoïd monkeys, and in 16 out of 43 sets for apes.

Only in a few cases of same-sexed twin pairs has the determination of zygoty actually been attempted. Examination of the ovaries and/or the placental membranes was conducted in some instances (HEIN *et al.*, 1985; SAPKAL, 1984; VAN WAGENEN, 1972; WISLOCKI, 1939). This evidence, however, may sometimes be ambiguous (HENDRICKX *et al.*, 1968; WISLOCKI, 1939; see also SAPKAL, 1984). Moreover, as the afterbirth is usually consumed, in most cases by the mother, examination of the placental membranes is often not possible.

In five cases, zygoty in same-sexed twins was evaluated by comparison of morphological characteristics (ABEL, 1933; BURTON & DE PELHAM, 1979; FLEISCHHACKER, 1968; NAKAMICHI, 1983; ROSEN, 1972). With one exception, the diagnosis in each of these studies was in favour of dizygotic (= fraternal) twins. In two cases, the evidence was ambiguous (ABEL, 1933; NAKAMICHI, 1983).

In six out of 12 sets of same-sexed twins, investigation of the type of twinning resulted in supporting dizygoty (BURTON & DE PELHAM, 1979; FLEISCHHACKER, 1968; GOODALL, 1983, 1986; GRZIMEK *et al.*, 1968; HANNA & JULY, 1983; KIRCHSHOFER *et al.*, 1968; ROSEN, 1972; VALERIO *et al.*, 1969), but the method used has not been described in each case.

Six cases of monozygotic (= identical) twins have been reported: two sets in *Macaca mulatta* (VAN WAGENEN, 1968a, 1972) and one set each in *M. arctoides* (CHRISTIE, 1969), *M. fascicularis* (HEIN *et al.*, 1985), *Presbytis entellus* (SAPKAL, 1984), *Pan troglodytes* (BOURNE, 1967), the latter being part of a triple birth. In addition, two cases of conjoined or incomplete twins have been reported, one for *Maeaca fascicularis* (BOLK, 1926) and one for *M. mulatta* (HARTMAN, 1943). Including these double monsters, also considered as monozygotic twins by SCHULTZ (1948, 1956), BREITINGER (1951) and BENIRSCHKE (1986), the available evidence amounts to eight cases.

It seems that monozygotic twins are very rare in comparison with dizygotic ones: The six cases of identical twins (without double monsters) correspond to 13.3% of the 45 sets with known zygoty. However, this proportion is influenced by the fact that dizygotic twins are more readily recognized (at least the pairs of unlike sex). As zygoty is unknown in a large part (80.6%) of the same-sexed twins (n = 62 sets without double monsters), the actual number of monozygotic twins may be underestimated.

Table 2 gives the number of sets of twins consisting of a) two males (MM), b) one

TABLE 2 – Number of twin sets consisting of two males (MM), of one male and one female (MF), and of two females (FF), respectively, for each species separately.

Species	References	Twin type		
		MM	MF	FF
<i>MACACA</i>				
<i>arctoides</i>	CHRISTIE, 1969	1		
<i>fascicularis</i>	ANONYMOUS, 1982	1		
	HEIN <i>et al.</i> , 1985			1
<i>fuscata</i>	RUDAT, 1948	1		
	MATSUI, 1979, cited in NAKAMICHI, 1983	1		
	NAKAMICHI, 1983		1	
<i>mulatta</i>	ASANOW & LIPPERT, 1976	2	3	1
	HENDRICKX & NELSON, 1971		1	1
	KOFORD <i>et al.</i> , 1966	1		
	RAWLINS <i>et al.</i> , 1984		1	
	SPENCER-BOOTH, 1968			1
	TAUB, 1983	2	2	
	VALERIO <i>et al.</i> , 1969	1		
	VAN WAGENEN, 1972		1	2
<i>radiata</i>	HENDRICKX & NELSON, 1971			1
<i>sylvanus</i>	SCHAUB, 1987	1	2	1
<i>PAPIO</i>				
<i>anubis</i>	HENDRICKX <i>et al.</i> , 1968	1		
<i>papio</i>	RAFERT & VOJIK, 1983			1
<i>hamadryas</i>	ABEL, 1933	1		
	ASANOW & LIPPERT, 1976	2	1	4
	BREITINGER, 1951	1		
	NOGGE, 1981	1		
	NOGGE, 1982		1	
<i>hamadryas</i> x <i>T. gelada</i>	ASANOW & LIPPERT, 1976	1	1	
<i>ERYTHROCEBUS</i>				
<i>patas</i>	ASANOW & LIPPERT, 1976	1		
<i>PRESBYTIS</i>				
<i>entellus</i>	MOHNOT & MOHNOT, 1982	1	2	
	SAPKAL, 1984			1
<i>melalophos</i>	BENNETT, 1988			1
<i>NASALIS</i>				
<i>larvatus</i>	WISLOCKI, 1939		1	
Total for Cercopithecoidea		20	17	15

(continued)

TABLE 2 (continued)

Species	References	Twin type		
		MM	MF	FF
<i>HYLOBATES</i>				
<i>lar</i>	SWIGERT, 1983			1
<i>syndactylus</i>	SCHMIDT, in press	2		1
<i>PONGO</i>				
<i>pygmaeus</i>	JONES, 1982	1	6	1
<i>GORILLA</i>				
<i>gorilla</i>	HANNA & JULY, 1983	1		
	KIRCHSHOFER <i>et al.</i> , 1968			1
	ROSEN, 1972	1		
	SABATER-PI, 1982		1	
	WATTS & HESS, 1988			1
	YERKES PRIMATE CENTER, RECORDS (1981), unpubl.	1		
<i>PAN</i>				
<i>trogodytes</i>	GEWALT & MASSETER, 1977; and Mr F. Ostenrath, pers. comm.		1	
	GOODALL, 1979	1		
	HEDIGER & ZWEIFEL, 1962		1	
	GEISSMANN, 1990	6	5	5
	MAUERHOFER, 1983, and pers. comm.			1
	ROBINSON, 1987	1		
	SCHULTZ, 1948	1	1	
	SHTEFKO, 1940		1	
	YAMAMOTO, 1967	1		
Total for Hominoidea		16	16	11

mule and one female (MF), and c) two females (FF). Compared with a random combination of the sexes (MM:MF:FF = 1:2:1), the proportion of sets of MF twins is significantly lower in the cercopithecoïd sample and in the combined catarrhine sample (Chi-square tests, $df = 2$, $p < 0.05$ in both comparisons), but not in the hominoid sample ($p > 0.10$). This provides indirect evidence of the existence of a substantial proportion of homozygotic sets in at least the cercopithecoïd twin sample.

The frequencies of monozygotic and dizygotic twins can be estimated from the information about the number of twins of like and unlike sex. If the sex ratio is 1/2, then half the dizygotic twins will, on average, be like-sexed. The number of monozygotic twins can therefore be estimated by subtracting the number of unlike-sexed twins, which are listed as MF in *Table 2*, from the number of like-sexed twins: (MM + FF) – MF. This method is usually known as ‘Weinberg’s method’ or ‘difference method’ (WEINBERG, 1901-02, p. 369f). The frequently used expression ‘differential method’ stems from an erroneous translation of WEINBERG’s «Differenzmethode» (ALLEN, 1981).

TABLE 3 – Number of twin sets consisting of two males (MM), of one male and one female (MF), and of two females (FF), respectively, and the estimated proportion of monozygotic twins, calculated from the total number of twin sets (N).

	Number of twin sets			N	Monozygotic twins (%)	
	MM	MF	FF		(¹)	(²)
Cercopithecoidea	20	17	15	52	34.6	34.0
Hominoidea	16	16	11	43	25.6	24.6
Total (Catarrhini)	36	33	26	95	30.5	29.7

¹ Difference method (WEINBERG, 1901-02).

² Method of maximum likelihood (see WATERHOUSE, 1950, or GITTELSON & MILHAM, 1964, 1965).

The number of monozygotic twins estimated by the difference method is 18 out of 52 sets (34.6%) for cercopithecoids, 11 out of 43 (25.6%) for hominoids, and 29 out of 95 (30.5%) for the combined sample of catarrhine monkeys and apes (*Table 3*). The estimate for the hominoid sample is not significantly lower than for the cercopithecoid sample (Chi-square test, $df = 1$, Chi square = 0.906, $p > 0.30$).

The proportion of monozygotic twins calculated from the total number of twin maternities varies considerably between human populations (from about 9 to 65%, see e.g. Friksson, 1973, p. 16), and the tentative estimates for Old World monkeys presented here fall well within this range. However, the situation may be different for other groups of primates: «All, or practically all, twinning may be dizygotic in prosimians, as it is in marmosets and sheep.» (PASZTOR & VAN HORN, 1979, p. 229; see also PASZTOR & VAN HORN, 1976, p. 336).

A modification of the difference method which does not assume a sex ratio of 1:1, the method of maximum likelihood (WATERHOUSE, 1950, or GITTELSON & MILHAM, 1964, 1965), was also applied to the same data set (*Table 3*). The results are similar to that of the difference method. The percentage of homozygotic twins estimated was 34.0% for cercopithecoids, 24.6% for hominoids, and 29.7% for the combined samples.

The estimates presented here can only be very rough approximations. This is due not only to the small sample sizes, but also to the fact that the various catarrhine species are unequally represented in the samples used to estimate the proportions of monozygotic and dizygotic twins. For instance, two species make up 58% of the cercopithecoid sample (*Macaca mulatta*: 37%, and *Papio hamadryas*: 21%), and one species, the chimpanzee, contributes 58% to the hominoid sample (see *Table 2*). Further, the assumptions underlying the difference method have been critically discussed, for instance by BULMER (1976), JAMES (1979), ALLEN (1981), and BOKLAGE (1985), and the latter three authors raise serious objections regarding the accuracy of the method.

The rate of monozygotic and dizygotic twin births in the total number of maternities can also be estimated, if the twinning frequency is known. Such an estimate, although tentative, is presented at the end of chapter 8.

Complications in gestation and birth

In humans, twins are known to be subject to both an increased risk of perinatal death (e.g. BARR & STEVENSON, 1961; CHANDRA & HARILAL, 1978; GITTELSOHN & MILHAM 1965; Leetz, 1976; NAEYE *et al.*, 1978; SELVIN, 1972; YERUSHALMY & SHEERAR, 1940), and a greater likelihood of certain congenital malformations, as compared to singletons (e.g. HAY & WEHRUNG, 1970; LAYDE *et al.*, 1980; MYRIANTHOPOULOS, 1976).

Large litter size has been cited as one of the principal causes of neonatal death in some strepsirhine primates (Lemuridae) (BENIRSCHKE *et al.*, 1985). For nonhuman catarrhine primates, at least in captivity, multiple pregnancies have been commonly reported to result in miscarriage, stillbirth or premature birth of one or both fetuses (e.g. HENDRICKX & NELSON, 1971; KEELING & ROBERTS, 1972). However, it has apparently not been demonstrated that perinatal death of Old World monkeys and apes is actually more frequent for twins than for singletons, with one exception: In chimpanzees (*Pan troglodytes*), SEAL *et al.* (1985) found that twins have a greater risk of perinatal death than single births (see below).

In humans, twins (especially the second born) have been reported to be more likely to die or to show marked neurological and behavioural disorders as a result of perinatal hypoxia (NAEYE *et al.*, 1978; ZAHÁLKOVÁ, 1978). Perinatal hypoxia has also been suspected to account for the similar deficits displayed by the second born of a pair of twin orangutans (SAVAGE, 1982; SAVAGE & SNOWDON, 1982).

Congenital disorders have been reported for catarrhine primates in five cases:

- one of two aborted (nearly term) fetuses in a white-throated guenon (*Cercopithecus albogularis*) was deformed (Wislocki, 1939);
- one of two prematurely and stillborn rhesus monkey twins showed complex teratological defects (LAPIN & YAKOVLEVA, 1963);
- in a set of stillborn male twins in *Macaca arctoides*, one infant was normal, except for small size, the other one was anencephalic (CHRISTIE, 1969);
- one animal of a set of monochoorial twins in *M. fascicularis* was grossly malformed. It lacked the head, upper extremities and heart, but showed large vascular anastomoses to the other, normal twin. This congenital anomaly (acardius acephalus) is very rare in humans and has been reported only from multiple-birth gestations, most commonly monozygotic twins (HEIN *et al.*, 1985);
- in a triple birth in a chimpanzee, two of the infants were stillborn and had never developed a brain (ROSENTHAL, 1981).

Two instances of so-called double-monsters (conjoined twins) have been found in stillborn macaques. The specimen reported by BOLK (1926) in *M. fascicularis* had two

heads, two trunks, two vertebral columns (including tails), two pairs of arms, but only one pair of legs (an ileopagus, according to the classification in GEDDA, 1951, 1961). The *Macaca mulatta* specimen of HARTMAN (1943; see also the figures in SCHULTZ, 1956, 1972) represented a less complete duplication: it had two partly united heads and a doubling of the spinal column from the mid-thoracic region upward (teratodymus).

In *Table 4*, twin births with known outcome are listed for each species. Triple births and double monsters are not included, since they have been treated previously. Infants which died within one month (30 days) after birth are considered here as representing reproductive failure and are listed in a separate column; twins which died later are listed as surviving offspring in the table. Of course, death of a twin need not be related to the twinning situation itself. A sharp distinction cannot usually be drawn and was not attempted. Therefore, in *Table 4*, the column of infants which died within one month after birth contains also one baboon twin (*Papio hamadryas*) bitten to death at the age of 12 days by an adult male (HEDIGER & ZWEIFEL, 1962).

Of 104 individual twin infants of Cercopithecoidea (Old World monkeys), only 53 (51.0%) survived, whereas 41 (39.4%) were aborted or stillborn, and 10 (9.6%) died within one month after birth. Of 84 twin infants of Hominoidea, 49 (58.3%) survived. Aborted and stillborn infants make up 23 (27.4%), and the infants which died within one month after birth amount to 12 (14.3%). From this, it might seem that in captivity Hominoidea twins have a slightly higher chance of surviving than the Cercopithecoidea twins. The difference is, however, not significant (Chi-square test, $df = 2$, $p > 0.10$).

For several colonies of Old World monkeys, combined rates of stillbirths and abortions in single births have been provided (see e.g. KUSHNER *et al.*, 1982; RAWLINS *et al.*, 1984; SMALL, 1982). These values show considerable variation: they range between 4.3-52.3% of conceptions, several of the values being close to the value for Old World monkey twins (39.4%). A comparison within only one species (*Macaca mulatta*) again gives ambiguous results. The rate of abortions and stillbirths in twins, as derived from *Table 4*, is 31.8% (7 in 22 twins). A significant difference (Chi-square test, $df = 1$, $p < 0.025$) was found in comparison with the reported number of 80 stillbirths and abortions in 616 conceptions of laboratory bred mothers (VALERIO *et al.*, 1969), and in another comparison ($p < 0.0005$) with the reported 4.3% of stillbirths and abortions in 1171 births of the Cayo Santiago colony (RAWLINS *et al.*, 1984). In comparison with other rates (141 in 612, and 75 in 401 conceptions, HENDRICKX & NELSON, 1971, and VAN WAGENEN, 1972, respectively), however, no significant difference was found (Chi-square tests, $df = 1$, $p > 0.1$). In the samples for single births (HENDRICKX & NELSON, 1971; RAWLINS *et al.*, 1984; VALERIO *et al.*, 1969; VAN WAGENEN, 1972), a few twin births are also included and had to be removed for comparison with the present sample of twin births. In those samples where the outcome of the twin births has not been reported (HENDRICKX & NELSON, 1971; RAWLINS *et al.*, 1984; VALERIO *et al.*, 1969), all known twin births were regarded as abortions and subtracted, in order to compare our rate for twins with the *minimal rate* for singletons. In one colony (HENDRICKX & NELSON, 1971), the rate of stillbirths and abortions is based on a sample of 612 conceptions. The exact number of twin births in this sample has not been provided, but the authors recorded 4 pairs of twins in a larger sample of 840 births. The rate of stillbirths and abortions in this colony does not differ significantly from the present sample of twin births, irrespective of whether a correction for 4 sets of twins is made or not.

In the rhesus monkey, neonatal deaths on or before 30 days of age have been reported to occur in 10.8% or 80 in 742 live births (HIRD *et al.*, 1975). This rate is again not statistically different (Chi-square test, $df = 1$, $p > 0.20$) from the corresponding

TABLE 4 – *Outcome of twin births in nonhuman catarrhine primates.*

Species	References	Pairs (p), individuals (i)			Total number of twin pairs
		Survived	Aborted/ stillborn	Died within 1 month	
<i>MACACA</i>					
<i>arctoides</i>	CHRISTIE, 1969		1p		1
	HENDRICKX & NELSON, 1971		1p		1
<i>fascicularis</i>	HEIN <i>et al.</i> , 1985		1p		1
	RUDAT, 1948	1i		1i	1
<i>fuscata</i>	MATSUI, 1979, cit. in NAKAMICHI, 1983	1p			1
	NAKAMICHI, 1983	1p			1
<i>mulatta</i>	ASANOW & LIPPERT, 1976	2p2i	1p1i	1i	5
	HENDRICKX & NELSON, 1971		2p		2
	SPENCER-BOOTH, 1968	1p			1
	VAN WAGENEN, 1972	3p			3
<i>sinica x radiata</i>	HAMERTON, 1937		1p		1
<i>sylvanus</i>	SCHAUB, 1987	1p1i	4p	2p1i	8
<i>PAPIO</i>					
<i>hamadryas</i>	ABEL, 1932, 1933		1p		1
	ASANOW & LIPPERT, 1976	3p	3p	1p	7
	BREITINGER, 1951	1p			1
	BUNGARTZ, 1949	1p			1
	HEDIGER & ZWEIFEL, 1962	1i		1i	1
	NOGGE, 1981, 1982, 1983	3p			3
<i>hamadryas x T. gelada</i>	ASANOW & LIPPERT, 1976		2p		2
<i>papio</i>	RAFERT & VOJIK, 1983	1p			1
<i>usrinus</i>	FITZSIMONS, 1919	1p			1
<i>CERCOPITHECUS</i>					
<i>albogularis</i>	WISLOCKI, 1939		1p		1
<i>pygeiythrus</i>	FITZSIMONS, 1919	1p			1
<i>sabaeus</i>	STOTT, 1946		1p		1
<i>ERYTHROCEBUS</i>					
<i>patas</i>	ASANOW & LIPPERT, 1976		1p		1
<i>PRESBYTIS</i>					
<i>entellus</i>	HRDY, 1976	3p			3
<i>melalophos</i>	BENNETT, 1982, 1988	1p			1
Total for Cercopithecoidea		24p5i	20pli	3p4i	52

(continued)

TABLE 4 (continued)

Species	References	Pairs (p), individuals (i)			Total number of twin pairs
		Survived	Aborted/ stillborn	Died within 1 month	
<i>HYLOBATES</i>					
<i>lar</i>	ELLEFSON, 1974	1p			1
	MOOTNICK, 1984	1p1i	1i		2
<i>syndactylus</i>	SCHMIDT, in press	2p1i	1i		3
<i>PONGO</i>					
<i>pygmacus</i>	JONES, 1982	6p2i	1p1i	1i	9
<i>GORILLA</i>					
<i>gorilla</i>	KIRCHSHOFER <i>et al.</i> , 1968	1p			1
	ROSEN, 1972		1p		1
	SABATER-PI, 1982	1i		1i	1
	WATTS & HESS, 1988			1p	1
	YERKES PRIMATE CENTER, RECORDS (1981), unpubl.		1i	1i	1
<i>PAN</i>					
<i>trogloodytes</i>	GEISSMANN, 1990	4p6i	4p4i	1p4i	16
	GOODALL, 1979	1p			1
	HEDIGER & ZWEIFEL, 1962	1i	1i		1
	MAUERHOFER, 1983	1p			1
	ROBINSON, 1987	1i		1i	1
	SHTEFKO, 1940		ip		
	YAMAMOTO, 1967	1p			
Total for Hominoidea		18p13i	7p9i	2p8i	42

value for cercopithecoïd twins (15.9% or 10 in 63 live births, see *Table 4*).

It can therefore be stated that convincing evidence for a higher perinatal mortality rate in cercopithecoïd twins is lacking. The failure to find a consistent difference between perinatal mortality in twins and single births may be due to the small sample sizes and to the fact that comparison was made with data derived from several species and colonies. It has been demonstrated that perinatal mortality within a colony of rhesus macaques may vary with different caging conditions (HIRD *et al.*, 1975), and with the proportion of imported pregnant monkeys to laboratory-bred mothers (VALERIO *et al.*, 1969). Considerably better data are required before any definite conclusions can be drawn.

Some evidence for higher perinatal mortality is, however, available for chimpanzees. A within-colony comparison of perinatal mortality is possible for the colony at the Yerkes Regional Primate Research Center. The outcome in single conceptions can be computed from the separately listed data on pregnancy outcome in all conceptions and in multiple conceptions only (MARTIN 1981, pp. 346 and 349). The rate of abortions and stillbirths is higher in twins (31.8% or 7 in 22 conceptions) than in singletons (12.9% or 36 in 279

conceptions); the difference is statistically significant (Chi-square test, $df = 1$, $p < 0.025$).

A re-analysis of the data extracted directly from the record files of the Yerkes Primate Center shows that some of the information on twin survival provided by MARTIN (1981, p. 349) must be inaccurate. For instance, the first twin in MARTIN's (1981) list (a male born in 1933) is stated to have died after 182 days; in fact, it died in 1948 at the age of about 15 years. The twin sister of this male is said to have died after 457 days, whereas she was actually traded in 1970, still alive, at the age of about 36.5 years! Several similar errors occur in this list, and a corrected and updated version of it will be published elsewhere (GEISSMANN, 1990). For the analysis of *perinatal* death, however, only one twin changes its position. The corrected rate of stillbirths thus becomes 36.4% (or 8 out of 22 conceptions), and the evidence for a higher perinatal mortality in this sample of twins becomes even more significant (Chi-square test, $df = 1$, $p < 0.005$).

SEAL *et al.* (1985) analysed relatively large samples of twins in chimpanzees (22 sets in 1311 births), gorillas (two sets in 246 births), and orang-utans (seven sets in 626 births), which were extracted from international studbooks and from ISIS (International Species Information System). These authors found that «chimpanzee twins have a two- to fourfold greater risk of being stillborn or dying the day of birth (34% vs 8.9%, $G = 20.56$, $p << 0.01$) and of dying in the first year (45% vs 8.9%, $G = 21.0$, $p << 0.01$) than single births.» In orang-utan twins, no significant difference was found, but this may be due to the small sample size. No statistical test could be carried out for the gorilla sample, since only two twin births were included in these records.

The present report includes slightly larger sample of twins for the latter two species: In 9 sets of orang-utan twins, 3 individuals were aborted or stillborn, and in 5 sets of gorilla twins, 3 individuals were aborted or stillborn (see *Table 4*). The samples of single births used by SEAL *et al.* (1985) can be calculated by subtraction of their samples of multiple births from their total samples of births, for each species, respectively. A comparison of perinatal mortality between these single births and the twin samples of the present investigation fails to yield evidence for a higher rate of stillbirths and abortions in twins (Fisher exact probability test, $p > 0.2$ for orang-utans, $p > 0.3$ for gorillas).

At least in captive chimpanzees, therefore, twin offspring seem to be at considerable risk at birth. It has been suggested that this may also apply to mothers of twins in various primates (BREITINGER, 1951; FLEISCHHACKER, 1968). The evidence for this is scarce, however, and cannot be statistically evaluated. In one case of an orang-utan twin birth, one placenta was retained and the mother developed a severe postparturient endometritis (ANONYMOUS, 1978c, d). In two cases, the mother actually died during or after the birth of twins:

– A bonnet macaque (*Macaca radiata*), pregnant by a toque macaque (*M. sinica*), died in labour. At necropsy the uterus was found to contain two fully developed normal fetuses and was in a condition of paralytic over-distension. «It appeared that labour had commenced, but had not progressed because of uterine inertia» (HAMERTON, 1937). It is unknown whether the condition of an interspecific hybridization may have influenced the outcome of this pregnancy.

– SHTEFKO (1940), SHTEFKO and KHAR'KOV (1946), and TSVETAYEVA (1941, cited in LAPIN & YAKOVLEVA, 1963) reported on a female chimpanzee which died from eclampsia without convulsions, four days after the premature delivery of twins which survived only a few hours. The development of the female's pathological condition was possibly enhanced by the double pregnancy (SHTEFKO & KHAR'KOV, 1946).

In *Table 5*, the outcome of twin births is presented for the twin pairs of known sex.

TABLE 5 – Outcome of twin births of sets with known sex in nonhuman catarrhine primates. MM, MF, and FF correspond to sets consisting of two males, of one male and one female, and of two females, respectively.

Species	References	Individuals			Total number of twin pairs	
		Survived	Aborted/ stillborn	Died within 1 month		
<i>MACACA</i>						
<i>arctoides</i>	CHRISTIE, 1969		MM		1	
<i>fascicularis</i>	Hein <i>et al.</i> , 1985		FF		1	
	RUDAT, 1948	M		M	1	
<i>fuscata</i>	MATSUI, 1979, cit. in NAKAMICHI, 1983	MF			1	
	NAKAMICHI, 1983	MM			1	
<i>mulatta</i>	ASANOW & LIPPERT, 1976	M	M		5	
		MF				
		MF				
		F		M		
			FF			
	HENDRICKX & NELSON, 1971		MF		2	
			FF			
	SPENCER-BOOTH, 1968	FF			1	
	VAN WAGENEN, 1972	MF			3	
		FF				
		FF				
<i>sylvanus</i>	SCHAUB, 1987		FF		4	
			MM			
		F		M		
		MF				
<i>PAPIO</i>						
<i>hamadyas</i>	ABEL, 1932, 1933		MM		1	
	ASANOW & LIPPERT, 1976	MM	MM		7	
			MF			
		FF	FF	FF		
		FF				
	BREITINGER, 1951	MM			1	
	NOGGE, 1981	MM			1	
	NOGGE, 1982	MF			1	
<i>hamadyas</i> x <i>T. gelada</i>	ASANOW & LIPPERT, 1976		MM		2	
			MF			
<i>papio</i>	RAFERT & VOJIK, 1983	FF			1	
<i>ERYTHROCEBUS</i>						
<i>patas</i>	ASANOW & LIPPERT, 1976		MM		1	
<i>PRESBYTIS</i>						
<i>melalophos</i>	BENNETT, 1988	FF			1	
Individuals from						
		MM sets	10	13	1	12
		MFsets	14	6	2	11
		FF sets	14	10	2	13
Total for Cereopithecoidea			38	29	5	36

(continued)

TABLE 5 (continued)

Species	References	Individuals			Total number of twin pairs
		Survived	Aborted/ stillborn	Died within 1 month	
<i>HYLOBATES</i>					
<i>lar</i>	SWIGERT, 1983; MOOTNICK, 1984	FF			
<i>syndactylus</i>	SCHMIDT, in press	M MM FF	M		3
<i>PONGO</i>					
<i>pygmaeus</i>	JONES, 1982	M M MF MF MF MF FF	M	F	8
<i>GORILLA</i>					
<i>gorilla</i>	KIRCHSHOFER <i>et al.</i> , 1968	FF			1
	ROSEN, 1972		MM		1
	SABATER-PI, 1982	F		M	1
	WATTS & HESS, 1988			FF	1
	YERKES PRIMATE CENTER, RECORDS (1981), unpubl.		M	M	1
<i>PAN</i>					
<i>trogodytes</i>	GEISSMANN, 1990	M M M MM MF M F FF FF	M M M MM	M M F M M MF	16
	GOODALL, 1979	MM			1
	HEDIGER & ZWEIFEL, 1962	F	M		1
	MAUERHOFER, 1983, and pers. comm.	FF			1
	ROBINSON, 1982	M		M	1
	SHTEFKO, 1940			MF	1
	YAMAMOTO, 1967	MM			
Individuals from					
	MM sets	15	9	4	14
	MF sets	17	5	6	14
	FF sets	14	6	2	11
Total for Hominuides		46	20	12	39

Among 66 twins (of known sex) which did not survive longer than one month (including stillbirths and abortions), the proportion was 38 males to 28 females (19:15 in Old World monkeys and 19:13 in apes). The difference is not statistically significant (Chi-square test, $df = 1$, $p > 0.10$). Of 77 males in twin pregnancies, 28 (36.3%) were aborted or stillborn, and 10 (13.0%) died during their first month after birth. Of 73 females in twin pregnancies, the number of aborted or stillborn individuals is 21 (28.8%); and 7 (9.6%) more females died within the first month post partum. These numbers are very small and do not suggest a male-female difference in mortality (Chi-square test, $df = 2$, $p > 0.30$). The results are similar if the cercopithecoid and the hominoid sample are tested separately ($p > 0.40$, and $p > 0.70$, respectively).

Of 50 twin sets of like sex, 38 individuals (38.0%) were aborted or stillborn, and 9 (9.0%) died within one month after birth. The corresponding numbers for 25 pairs of unlike sex are 11 (22.0%) aborted or stillborn animals and 8 (16.0%) animals which died within one month after birth. In the combined sample of catarrhine twins, sets of like sex were found to show an excess of abortions and stillbirths, as compared to the rate in pairs of unlike sex (Chi-square test, $df = 1$, $0.025 < p < 0.05$). This result is not obtained if the cercopithecoid and hominoid samples are tested separately, perhaps because of the small sample sizes ($0.05 < p < 0.10$, and $0.10 < p < 0.20$, respectively).

An excess of perinatal mortality in same-sex pairs of twins has also been found in human populations (BOKLAGE, 1985; HAY & WEHRUNG, 1970; HOFFMANN *et al.*, 1978; LAYDE *et al.*, 1980; MYRIANTHOPOULOS, 1970; SELVIN, 1972; YERUSHALMY & SHEERAR, 1940). This finding has usually been interpreted as a result of selection against monozygotic twins during the perinatal period (BARR & STEVENSON, 1961; GITTELSON & MILHAM, 1965; NAEYE *et al.*, 1978; SELVIN, 1972; YERUSHALMY & SHEERAR, 1940). However, BOKLAGE (1985) also presented evidence suggesting that an excess in the mortality of same-sex twins may be at least partially related to the same-sex condition itself. The small number of nonhuman twins does not permit comparable conclusions.

Complications in postnatal development and rearing

In captivity, as mentioned in the previous chapter, twins are often born prematurely, thus frequently making handraising necessary (e.g. ANONYMOUS, 1981; BOND & BLOCK, 1982; OLSEN, 1976; YAMAMOTO, 1967). It seems unlikely that such young could survive in the wild. Even with term-born twins, additional problems (see below) may arise for both the mother and the twins; it has therefore been suggested that twins would experience difficulty in nature (HINDE, 1972).

In most catarrhine primates, newborn infants are carried clinging ventro-ventrally to the abdomen of their mother. In captive and in feral chimpanzees it has been reported that twins could not assume this natural position because of mutual interference. Often one would grasp the other with one or both of its extremities and as a result both would lose their grip on their mother and start to fall. They had to be given almost continuous support (GOODALL, 1979; TOMILIN & YERKES, 1935). «If as she moved about she [the mother] happened to withdraw the support, they usually sagged toward the floor» (TOMILIN & YERKES, 1935, p. 245) (*Figure 1a*).

WATTS and HESS (1988) reported on the maternal behaviour of a mother of female twins in feral mountain gorillas (*Gorilla gorilla beringei*): Initially, both daughters were carried ventrally and supported with one arm by the mother. When feeding, the mother cradled both infants ventrally with one arm while using the other arm to process food. When resting and lying on her back, she often held one infant against herself with one arm. However, from the fourth day after birth onward, both mother and twins appeared to experience increasing difficulties. The mother «had trouble supporting both infants while she walked, and often one had to cling unaided to her side» (WATTS & HESS, 1988, p. 6). Both twins were observed to cry increasingly often, especially during their mother's feeding bouts. While feeding, the mother was unable to provide both with warmth, comfort, and – most importantly – with access to a nipple. On the seventh day after birth, the mother abandoned one of the twins, which suffered from pneumonia and probably from starvation. It died within several hours. Two days later, the other twin also died (see also below).

In captive hamadryas baboons a mother seemed able to carry her twin offspring only with difficulty. She alternated between carrying them both together on one arm and carrying one on each arm. With the latter option, however, she was severely impeded, especially in climbing and feeding. As a result, she carried both offspring on her left arm

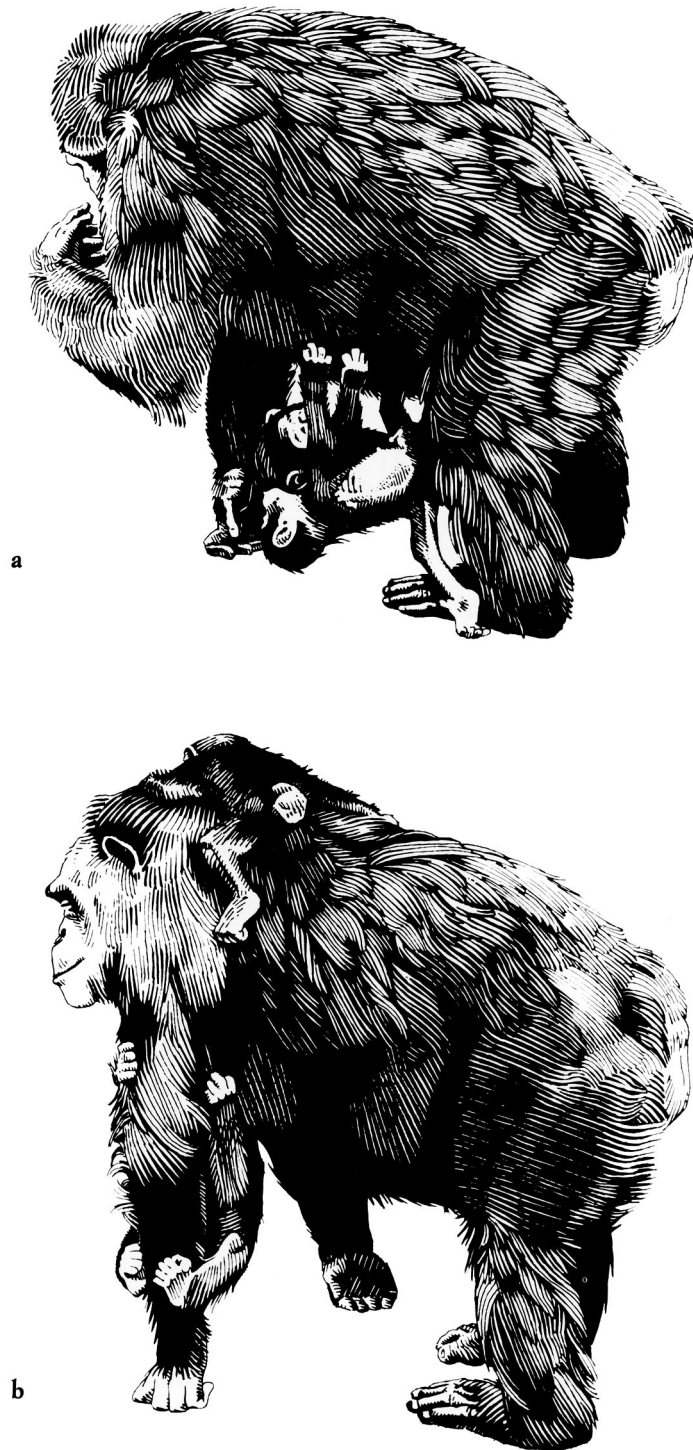


Figure 1. – A chimpanzee mother in captivity, carrying her twin offspring. (Based on photographs from TOMILIN and YERKES, 1935).

- a. At the age of two months, the twins still had difficulties in clinging to their mother's belly.
b. The carrying position preferred by the twins at the age of 27 weeks.

during these activities (HEDIGER & ZWEIFEL, 1962). A virtually identical observation, also with hamadryas twins, was made by BUNGARTZ (1949); initial difficulties in carrying twin offspring have also been reported for *Macaca fascicularis* (ANONYMOUS, 1970) and for *M. mulatta* (DEETS & HARLOW, 1974).

A mother in a feral group of banded langurs (*Presbytis melalophos*) in Peninsular Malaysia was also reported to experience difficulties in carrying and caring for her twin offspring: «When both of the twins were with her, she constantly supported them with one arm as she moved, and travelled using only three limbs. For such a highly arboreal and agile monkey, this is presumably difficult, tiring and potentially dangerous. It may also prevent her from obtaining food from more inaccessible sites.» (BENNETT, 1988, p. 561). However, some mothers of twins do not seem to have problems in carrying both infants simultaneously (e.g. observations by SCHAUB, 1987, on *Macaca sylvanus*). Interestingly, carrying difficulties in a mother of twins have recently been observed during a field study on a species of New World monkey (*Alouatta palliata*) (CHAPMAN & CHAPMAN, 1986).

However, such mechanical difficulties are not insurmountable. In a pair of chimpanzee twins, TOMILIN and YERKES noted that «degree of skill and success in grasping and holding to their mother's coat or skin increased steadily with strength and practice. It was only during the first month that embarrassments especially impressed the observers...» (TOMILIN & YERKES, 1935, p. 245).

Several twin pairs have been reported to show later preferences for special carrying positions which limited their mutual interference. The chimpanzee twins observed by TOMILIN and YERKES (1935) shifted their habitual position on the body of their mother during the fifth month. Whereas previously both had clung to the abdomen whenever possible, the male twin now by preference rode on his mother's back while his sister clung to an arm or leg (*Figure 1b*). EIFFERT (1951), reporting on the same hamadryas twins as BUNGARTZ (1949, see above), noted that the mother initially carried her infants both on one arm during locomotion. At a later stage of their development, however, one infant was carried ventro-ventrally while the other one rode on her back. NAKAMICHI (1983) observed male twins of the Japanese monkey (*Macaca fuscata*) during their first 12 months of life. They were carried simultaneously by their mother until 5 months of age. A pattern in which one clung dorsally and the other ventrally was observed most frequently.

Initial complications in carrying twin offspring seem to be a transitory phenomenon of relatively short duration, and may perhaps even be underrepresented in the reports to date. HRDY (1976) pointed out that monkeys can and do carry 2-3 offspring at a time. Nevertheless, the weight of an additional infant may slow down its mother's locomotion and eventually that of the whole troop. «Terrestrial primates that need to cover long distances during the day might find an extra infant an even greater burden than it is for more sedentary arboreal monkeys» (HRDY, 1976, p. 130). For chacma baboons (*Papio ursinus*), the risk associated with carrying two infants has been demonstrated in an example reported by FITZSIMONS (1919, p. 56f). A farmer and his sons, on horseback, surprised a troop of baboons raiding his fields. All monkeys but one got safely away to their stony, inaccessible retreat. One female could not keep pace with the troop. The reason for her inability became apparent, when her pursuers finally caught up with her: She was found to be carrying two infants and this circumstance proved to be fatal; the female was shot.

In several cases, both in captivity and in the field, mothers of twins seem to have been unable to provide sufficient milk for both offspring (GOODALL, 1979; HEINRICHS & DILLINGHAM, 1970; LANG, 1973; LAPIN & YAKOVLEVA, 1963; NOGGE, 1981). In one of these cases, the weaker infant of a pair of captive orang-utan twins died after hardly four

weeks (LANG, 1973). Of a pair of chimpanzee twins observed in the Gombe National Park, both suffered from malnutrition. Weak and highly susceptible to infection, one infant died at 10 months, probably of pneumonia (GOODALL, 1979, p. 616). Whereas in similar situations in captivity the infants may sometimes still be handreared, as has actually been done in many cases (e.g. BOND & BLOCK, 1982; KIRCHSHOFER *et al.*, 1968; LAPIN & YAKOVLEVA, 1963; NOGGE, 1981, 1982, 1983), such twins in the wild would probably perish. In fact, relatively few of the reports on twins listed in *Table 1* stem from observations on feral animals (BENNETT, 1982, 1988; ELLEFSON, 1974; FITZSIMONS, 1919; GOODALL, 1979, 1983, 1986; HRDY, 1976, 1977; ITANI, 1959; MOHNOT & MOHNOT, 1982; NAKAMICHI, 1983; RAHAMAN & PARTHASARATHY, 1969; WATTS & HESS, 1988).

An undernourished twin may have a better chance of survival if adopted by another lactating female. Females which had lost their own infants have been reported to set aggressively about obtaining a substitute (e.g. HRDY, 1976, p. 128). Nevertheless, there are apparently no published cases of successful adoption and rearing of a twin in free or semi-free ranging catarrhine primates. The fact that childless females often show great interest in newborn infants of other females is well-known. However, in hamadryas baboons at the Succhumi Primate Center, a mother of twins was constantly harassed by other females which had lost their own offspring and which constantly tried to take over one of the twins (ASANOW & LIPPERT, 1976). This mother was said to attract much more such interference than mothers with one offspring. Two days after the death of one twin, the interest shown by the other females in this mother declined to the level existing prior to the twin birth. ASANOW & LIPPERT (1976) suggested that twins may represent a superoptimal stimulus for childless females, which by their constant attempts to get possession of a twin offspring may further aggravate the stressful situation of the mother-infant trio.

In a feral group of banded langurs (*Presbytis melalophos*) in Peninsular Malaysia, the birth of female twins was observed to stimulate unusually large amounts of allomothering, a behaviour which was absent or very rare when single infants were born (BENNETT, 1988). Maltreatment of the twins by allomothers was common, even though this was never observed with single infants. It was «obviously difficult» for the mother to carry her offspring, and it was suggested that she allowed other animals to take one of the twins from her as a result of these difficulties. The twins were repeatedly abandoned by the allomothers and were usually retrieved rapidly by the mother.

In some cases, only one twin was born alive (HEDIGER & ZWEIFEL, 1962; HENDRICKX & NELSON, 1971; KEELING & ROBERTS, 1972; MARTIN, 1981; SCHMIDT, in press), or deliveries of twin infants occurred over an interval of several days (BURTON & DE PELHAM, 1979). In a twin birth of *Macaca fascicularis* in captivity, reported by RUDAT (1948), the first young, born prematurely, was weak and died, the second mature and strong twin was born 21 days later.

But even in those twinning events where both offspring were born alive and on the same day, remarkable differences between the offspring or the way they were treated have been mentioned in several reports. HENDRICKX *et al.* (1968, 1971), for instance, reported a developmental difference of seven days in a set of twin embryos of Kenyan baboons (*Papio* sp., assigned to *P. anubis* by HILL, 1970, p. 221). It is not uncommon that one twin is smaller and weaker than the other (e.g. Robinson, 1988; SCHAUB, 1987) and may die during infancy (e.g. ASANOW & LIPPERT, 1976; LANG, 1973; SABATER-PI, 1982). In a set of twin chimpanzees at Southport Zoo, the smaller of the twin males had to be removed on the seventh day after birth: «It had become progressively weaker, due to the larger twin inadvertently placing its arm across the mother's breast, which impaired access to the

nipple and as a consequence the smaller twin's suckling bouts decreased dramatically.» (ROBINSON, 1987, p. 145).

SAVAGE and SNOWDON (1982) argued that under certain circumstances, in the wild, there may be a greater likelihood of at least one infant surviving if the weaker or more disabled twin is allowed to die. In several cases, a mother was reported to discriminate between her offspring and to favour one twin more than the other. One twin received more maternal attention and assistance in connection with nursing, grooming and protection against its sibling, whereas the other twin was restrained and was struck more often (HINDE, 1969; MATSUI, 1979, cit. in NAKAMICHI, 1983; SPENCER-BOOTH, 1968; TOMLIN & YERKES, 1935). In the case of rhesus twins reported by SPENCER-BOOTH (1968) and HINDE (1969), both infants were females; in this instance, therefore, the preference of the mother for one twin cannot be ascribed to sexual differences between the infants.

In a troop of free ranging Japanese macaques (*Macaca fuscata*), one infant of a pair of twins was taken at one month postpartum and cared for by the mother's presumed mother. As this female did not breed that year, she had no milk and the baby died about a week later, apparently of starvation (ITANI, 1959).

There are very few instances in the literature of a mother of twins actually abandoning one of her infants. A female rhesus macaque at the Primate Laboratory, Wisconsin initially attempted to cradle her twin offspring both simultaneously, but one or both infants would become misaligned on the mother's belly or would slip to the floor, and by the morning of the third day afterbirth, the mother had abandoned one of the infants, which subsequently had to be cared for in the laboratory nursery (DEETS & HARLOW, 1974).

The second case of a mother abandoning one of her twin offspring was observed in a group of feral mountain gorillas (WATTS & HESS, 1988) and has already been mentioned earlier in this chapter. From the fourth day after birth, the mother («Walanza») appeared to have increasing problems in supporting both twins and in providing both with access to a nipple. «On day 7, Walanza left one of the twins behind when the group moved on after a midday rest. Several gorillas showed interest in the infant, which was still alive, but none attempted to care for it. The baby died within several hours. An autopsy showed that it had pneumonia and an empty gut – dramatic evidence of the severity of the mechanical problems that Walanza had in adequately providing both warmth and nourishment to two neonates simultaneously.» (WATTS & HESS, 1988, p. 6). Nevertheless, the second twin also died two days later, but this time, the mother carried the body for over two days before abandoning it.

In a laboratory study, DEETS and HARLOW (1974) separated 4 rhesus mothers from their newborn offspring and offered two other infants for adoption. These mothers again had difficulties in arranging both infants on their belly and in embracing them simultaneously (*Figure 2*). Many infants were rejected initially, although – with one partial exception – the mothers eventually accepted and cared for two infants. Three of the mothers demonstrated a preference for one of their artificial twins, which was still effective at reunion of the mothers with the infant pairs after a 3-week separation period one year postpartum. However, NAKAMICHI (1983) found no evidence that a female Japanese macaque (*Macaca fuscata*) preferred one of her twin offspring or differentiated between them.

The previous reports give some evidence that mothers with multiple offspring may indeed show preference for one of their infants and may neglect or even abandon the other. Such observations led DEETS and HARLOW (1974) to conclude that the macaque maternal affectional system may be biased toward accepting and rearing one infant at a time. In the case of ape mothers, it has even been questioned whether they are able to

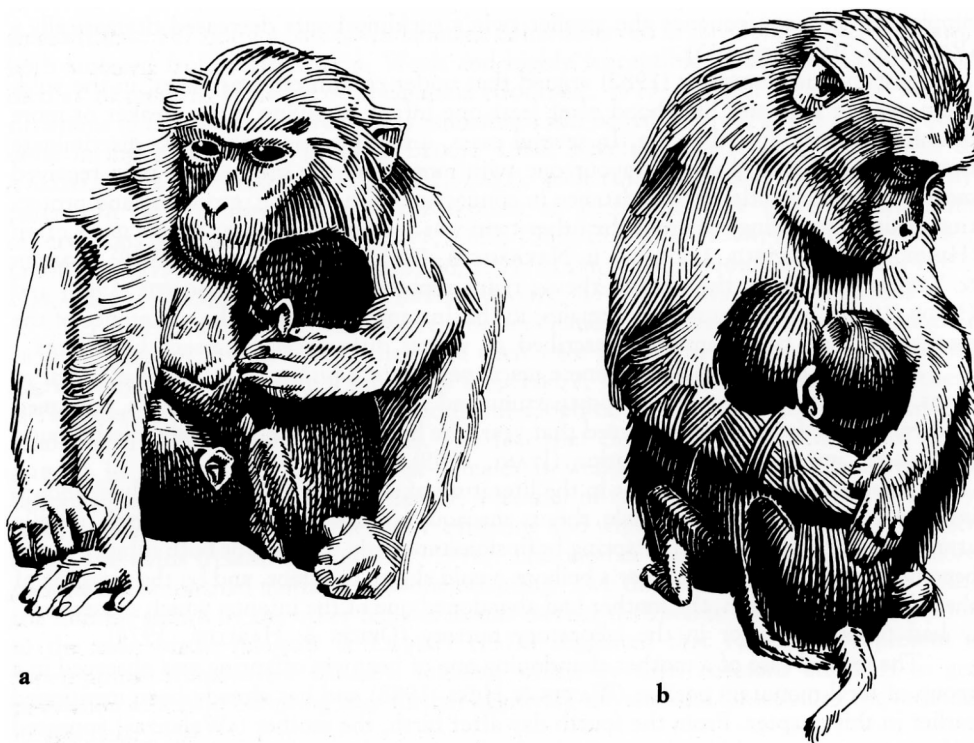


Figure 2. – Adoption of two infants by rhesus monkey mothers (*Macaca mulatta*), in a laboratory situation. (Based on photographs from DEETS and HARLOW, 1974).

a. Typical example of a mother's first attempts to cradle two infants simultaneously.

b. Typical example of maternal cradling after habituation to the twinned infants.

feed and care for twins (HENDRICKX & NELSON, 1971; KIRCHSHOFER *et al.*, 1968). However, several sets of twins in catarrhine monkeys and apes have been successfully reared by their own mothers until at least one year old. Such observations have been made not only with captive monkeys and apes (e.g. *Macaca mulatta*: SPENCER-BOOTH, 1968; *Papio hamadryas*: BUNGARTZ, 1949; EIFFERT, 1951; *Cercopithecus pygerythrus*: FITZSIMONS, 1919; *Pan troglodytes*: TOMILIN & YERKES, 1935) but also with free-ranging animals (e.g. *Macaca fuscata*: NAKAMICHI, 1983; *Presbytis entellus*: HRDY, 1976; *Hylobates lar*: ELLEFSON, 1974).

Several instances are known of mothers which, in addition to their own biological offspring, adopted an infant which was also nursed and cared for. Again, such cases have been reported both for captive animals (*Macaca arctoides*: ASANOW & LIPPERT, 1976; *M. fuscata*: FUCILLO *et al.*, 1983; *M. mulatta*: BREUGGEMAN, 1973, and KOFORD *et al.*, 1966; *M. nemestrina*: LAPIN & YAKOVLEVA, 1963; *Presbytis entellus*: DOLHINOW, 1980) and for feral monkeys (*Macaca fuscata*: KUROKAWA, 1974, cited in NAKAMICHI, 1983; *M. radiata*: JAY, 1965; *Presbytis entellus*: MOHNOT, 1980). One rhesus female in a free-ranging colony,

after having to care for two very young infants (one of which she had adopted), became very cautious, and avoided, as much as possible, the central part of her group. As the infants grew older, she frequently had both of them 'kidnapped' from her and seemed unable to keep track of both of them (BREUGGEMAN, 1973).

A female bonnet macaque (*M. radiata*), the mother of a 5-month-old, «successively adopted two other infants of comparable age that had been experimentally separated from their own mothers. She carried all three, albeit with some difficulty, sustained contact with all of them, and each nursed from her, usually two at a time» (ROSENBLUM, 1968, p. 228; see also KAUFMAN & ROSENBLUM, 1969) (*Figure 3*). JENSEN and BOBBITT (1968) also described a *Macaca nemestrina* mother, in a laboratory situation, that accepted two infants in addition to her natural offspring, and similar cases have also been reported for *M. fascicularis* (THOMMEN, 1974) and for *Presbytis entellus* (DOLHINOW, 1980).

From these reports, it is evident that some mothers will care for multiple infants and are successful in rearing them, even if they are not their own biological offspring. The present observations, however, do not provide an answer as to why multiple infants may be attractive to some mothers and not to others, why some mothers are successful in rearing them, while others are not, nor why some mothers will prefer one twin and restrain, neglect or even reject the other one, while other mothers do not seem to differentiate between their twin offspring.

Whereas SAVAGE and SNOWDON (1982) suggested that, under certain circumstances, the weaker twin should be allowed to die, TOMILIN and YERKES (1935) reported that the weaker female of a set of chimpanzee twins received «noticeably more maternal attention and assistance» than her twin brother. In the rhesus mothers which were offered two infants for adoption (see above), DEETS and HARLOW (1974) failed to find a consistent association of the adoption reaction with parameters such as time since parturition, age of the infants, or birth weight of the infants. For instance, in two of the artificial twin pairs offered, the heavier infant was rejected more frequently, but in another pair the opposite was true.

In a laboratory situation, CHO *et al.* (1986) separated 77 *Macaca fascicularis* mothers from their biological infants a few days (1.1 ± 3.5 days) after delivery, and then, on the same day offered *two* infants together to each of these mothers. One of these artificial twins was a foster infant; the other was the mother's returned biological infant. Age differences between the artificial twins ranged from 0 to 39 days (2.5 ± 6.0 days). Only if the mother accepted both infants handed to her and allowed ventral contact to both of them over seven observation days was the adoption judged successful. Neither the infants' age at adoption nor the interaction of biological versus foster infant with adoption age appeared to be significantly associated with success rate. Likewise, neither symmetry nor asymmetry in age between the biological and foster infant reliably affected adoption success, nor did pairings of the same or opposite sex. And finally, neither sex of the biological infant nor sex of the foster infant had significant effects (see CHO *et al.*, 1986).

DEETS and HARLOW (1974) suggested one possible explanation for the ambivalence which some mothers displayed toward multiple infants. If an infant's clinging is interpreted as providing a necessary feedback which stimulates and sustains maternal behaviour, then «the simultaneous presence of two infants on the mother's ventrum, clinging in a haphazard way to themselves as well as to the mother, may not provide the kind of infantile feedback that is maximally reinforcing for a monkey mother.» (DEETS & HARLOW, 1974, p. 199). The difficulty in establishing «mutual ventral clinging» with both infants at the same time may represent a crucial problem for females with two infants (see *Figure 1* and *2*).



Figure 3. – A bonnet mother (*Macaca radiata*) that adopted two experimentally separated bonnet infants of her group, in addition to her own infant of comparable age. (Based on a photograph from KAUFMAN and ROSENBLUM, 1969).

Mothers in catarrhine primates show a broad variability in the way they are reacting to twin offspring. Although several parameters have been proposed which possibly influence a mother's affectional relationship with multiple offspring, the limited size of the sample precludes linking of specific types of maternal behaviour to specific situations. The consistency of the finding that mothers preferred one infant of a set of twins, while being to some degree reluctant to accept the the other infant and to care for it, seems to

indicate that this is no abnormal maternal behaviour, but rather inherent to the maternal affectional system of macaques and possibly other catarrhine primates.

These observations show, in addition, a conspicuous resemblance to one of the many classic fables generally attributed to the Greek story-teller Aesop, who probably lived in the middle part of the sixth century B.C.:

«It is said that apes produce twins, on one of which they lavish affection, feeding it with great care, while they turn against the other and neglect it. But by a curious dispensation of providence, the one that the mother delights to care for and strains tightly to her breast is smothered to death, while the rejected one reaches maturity.» (attributed to Aesop, translated by S.A. HANDFORD, 1954, p. 51).

Other, but essentially similar versions of Aesop's fable can be found in the translations provided by CAMERARIUS (1576), GENT (1715, cited by REYNOLDS, 1967, p. 28) and RICHARDSON (1740, p. 146). The «apes» of these translations were in all probability cercopithecoïd monkeys, perhaps barbary macaques, *Macaca sylvanus* (see REYNOLDS, 1967, p. 28).

Aesop's fable of the monkey mother with twin infants was later adapted into a Christian morality tale and found wide distribution in bestiaries of the eleventh and twelfth centuries (e.g. REYNOLDS, 1967, p. 36; WHITE, 1960, see epigraph to this monograph). The story was unearthed again for the zoological compilation of GESNER (1551, p. 960) and its later translation by TOPSELL (1658, p. 4).

REYNOLDS (1967, p. 39) drew attention to reports that when a macaque infant happens to die, a mother may hold on to the baby's corpse and continue to carry it around for several days. Based on this, REYNOLDS suggested that «surely it was the sight of a mother Barbary ape clutching the corpse of her baby that gave rise to this story. The idea... of the hated twin on her back, belong[s], on the other hand, to the realm of fancy.» However, several of the observations quoted in this chapter agree with Aesop's classic fable in two points: the monkey mother prefers one twin over the other, and the twins are carried in different positions. These remarkable similarities may be more than coincidence.

Twinning frequency

Most estimates of twinning frequency in catarrhine primates stem from captive animals. In free-ranging primates, twins dying during the perinatal period (see chapter 6 on complications in gestation and birth) may more readily pass undetected than in captivity, and the occurrence of 'pseudo twins' may further obscure the picture.

TICKELL's (1864a, b) note on the white-handed gibbon (*Hylobates lar*) contains what may be considered one of the first estimates of twinning frequency in a catarrhine primate: «They [the young] are born generally in the early part of the cold weather, a single one at a birth, two being as rare as twins in the human race» (TICKELL, 1864a, p. 197f and 1864b, p. 362). Whereas DE SNOO (1942, p. 56) claimed that multiple pregnancies in macaques occurred much less frequently than in humans, several authors suggested that multiple births in all catarrhine primates (BREITINGER, 1951; GUTTMACHER, 1953; HARMS, 1956, p. 650; SCHULTZ, 1948, 1956, p. 1006, and 1969, p. 236; STARCK, 1974) or at least in the rhesus macaque (VAN WAGENEN & ASLING, 1964) occurred with a frequency that was approximately the same as in humans. In these reports, the percentage frequency of plural births in humans was thought to be somewhere near 1.28 (HARMS, 1956; SCHULTZ, 1948), 1.17 (SCHULTZ, 1956) or 1.11 (VAN WAGENEN, 1968a), which are values found in the population of the United States (e.g. STRANDSKOV, 1945). However, when greater birth samples became available, both SCHULTZ (1972) and VAN WAGENEN (1968a, 1972) suggested that twinning in Old World monkeys or at least in the rhesus macaque might be less frequent than previously thought, whereas PEACOCK and ROGERS (1959) and FLEISCHHACKER (1968) suggested that the apparent twinning rate in chimpanzees was higher than that in humans.

Twinning frequency in humans is not necessarily a biological constant. The value is known to differ between U.S. populations: «The 'colored' U.S. population has a significantly higher twin and triplet confinement frequency than does the 'white'» (STRANDSKOV, 1945, p. 55; see also HEUSER, 1967; KHOURY & ERICKSON, 1983; MOSTELLER *et al.*, 1981). Moreover, these values may be subjected to secular changes (HEUSER, 1967; JEANNERET & MACMAHON, 1962; MOSTELLER *et al.*, 1981). Even much greater differences have been observed between populations outside of the United States. Twin frequencies as low as 0.3% have been found among some Oriental populations, and extremely high frequencies with values up to 4-5% in some parts of West Africa (for a bibliography see ERIKSSON, 1973, p. 11ff).

The ideas of especially low twinning rates in Cercopithecoidea (e.g. BURTON & DE PELHAM, 1979; SCHRIER & POVAR, 1984) and of an especially high rate in the chimpanzee and the gorilla (ANONYMOUS, 1972; KIRCHSHOFER, cited in LANG, 1973; MARTIN, 1981;

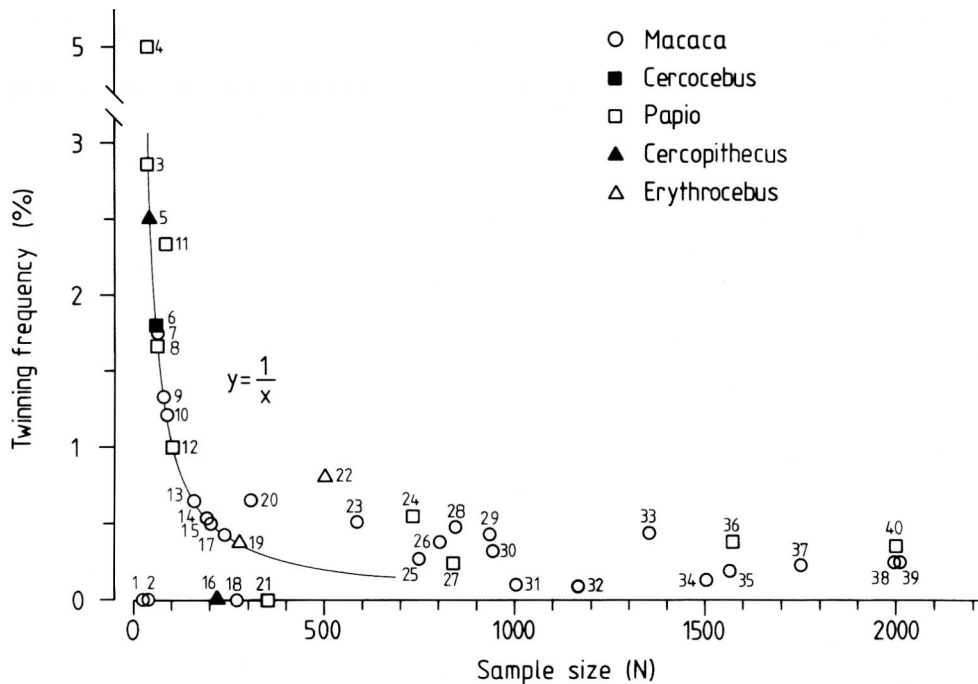


Figure 4. – Interdependence between sample size and twinning frequency in cercopithecoids. The list (see facing page) gives the source of each sample, the numbers in the figure correspond to the sample number in the list. Only samples of more than 20 births were used.

but see SEAL *et al.*, 1985) have been supported in more recent reports. Therefore, twinning frequency estimates for Old World monkeys and apes will be treated separately in the following. It should be noted, however, that the estimates are not evenly distributed among Old World monkey taxa, but rather concentrated on macaques and baboons. No estimate for any colobine monkey species was found in the literature.

8.1 Cercopithecoidea

Twinning frequency estimates for Old World monkeys may differ remarkably between authors. For instance, independent reports on *Macaca mulatta* suggest frequencies ranging from 0.09% (one twin set in 1171 births, RAWLINS *et al.*, 1984) to 0.51% (three twin sets in 583 pregnancies, VAN WAGENEN, 1972), or in *Papio hamadryas* from 0.35% (7 twin sets in 2000 births, ASANOW & LIPPERT, 1976) to 1.67% (one set in 60 births; ABEL, 1933).

Figure 4 presents published twinning frequency estimates for Old World monkeys. Where the relative frequencies were not provided, the twinning frequency was calculated from the data presented (Twinning frequency = the number of known twin sets divided by the number of known births, multiplied by 100). It should be noted that twinning rates

Legend to figure 4 (continued)

Sample number	Species	References	No. of twins	Sample size
1	<i>Macaca mulatta</i>	ABEL, 1933	0	24
2	<i>M. fascicularis</i>	ABEL, 1933	0	24
3	<i>Papio anubis</i>	SCHULTZ, 1948	1	35
4	<i>P. hamadyas</i> x <i>Theropithecus gelada</i>	ASANOW & LIPPERT, 1976	2	40
5	<i>Cercopithecus</i> spp.	STOTT, 1946	1	40
6	<i>Cercocebus torquatus</i>	HENDRICKX & NELSON, 1971	1	56
7	<i>M. arctoides</i>	BRÜGGEMANN & GRAUWILER, 1972	1	57
8	<i>P. hamadryas</i>	ABEL, 1933	1	60
9	<i>Macaca</i> sp.	HARMS, 1956	1	75
10	<i>M. arctoides</i>	HENDRICKX & NELSON, 1971	1	82
11	<i>Papio</i> spp.	SCHULTZ, 1948	2	86
12	<i>P. hamadryas</i>	RUDAT, 1948	1	100
13	<i>M. sylvanus</i>	BURTON & SAWCHUK, 1974	1	155
14	<i>Macaca</i> sp. = <i>M. mulatta</i>	SCHULTZ, 1948; HARMS, 1956	1	188
15	<i>M. radiata</i>	HENDRICKX & NELSON, 1971	1	199
16	<i>Cercopithecus aethiops</i>	KUSHNER <i>et al.</i> , 1982	0	221
17	<i>M. fuscata</i>	TANAKA <i>et al.</i> , 1970	1	234
18	<i>M. fascicularis</i>	HENDRICKX & NELSON, 1971	0	269
19	<i>Erythrocebus patas</i>	ASANOW & LIPPERT, 1976	1	273
20	<i>M. sylvanus</i>	PAUL & THOMMEN, 1984a, b	2	305
21	<i>Papio</i> hybr.	ASANOW & LIPPERT, 1976	0	350
22	<i>Erythrocebus patas</i>	SLY <i>et al.</i> , 1983	4	501
23	<i>M. mulatta</i>	VAN WAGENEN, 1972	3	583
24	<i>Papio</i> sp. = <i>P. anubis</i>	HENDRICKX <i>et al.</i> , 1968; HILL, 1970	4	730
25	<i>Macaca</i>	LAPIN & YAKOVLEVA, 1963	2	745
26	<i>M. mulatta</i>	PASZTOR & VAN HORN, 1976	3	800
27	<i>Papio</i> spp.	LAPIN & YAKOVLEVA, 1963	2	837
28	<i>M. mulatta</i>	HENDRICKX & NELSON, 1971	4	840
29	<i>M. mulatta</i>	TAUB 1983, GAREY <i>et al.</i> , 1985	4	928
30	<i>M. arctoides</i>	SCHRIER & POVAR, 1984	3	937
31	<i>M. mulatta</i>	KOFORD <i>et al.</i> , 1966	1	1003
32	<i>M. mulatta</i>	RAWLINS <i>et al.</i> , 1984	1	1171
33	<i>M. mulatta</i>	ASANOW & LIPPERT, 1976	6	1350
34	<i>M. mulatta</i>	COURTNEY & VALERIO, 1968	2	1500
35	<i>M. mulatta</i>	VALERIO <i>et al.</i> , 1969	3	1561
36	<i>Papio</i> spp.	WILDT & DUKELOW, 1974	6	1567
37	<i>M. mulatta</i>	KOFORD <i>et al.</i> , 1966	4	1748
38	<i>M. mulatta</i>	PASZTOR & VAN HORN, 1976	5	2000
39	<i>M. mulatta</i>	SCHRIER & POVAR, 1984	5	2000
40	<i>P. hamadryas</i>	ASANOW & LIPPERT, 1976	7	2000

in this review are based on the numbers of births (including abortions and stillbirths), not maternities. In this respect, I follow the common procedure in the primatological literature, in contrast to the method used in some reports on human twins (e.g. BULMER, 1970; ERIKSSON, 1973). This difference is, of course, accounted for in the following statistical comparison (see below).

Twinning frequencies have been plotted against sample size (see *Figure 4*). With samples of less than about 500 births, the estimates generally show two trends: 13 (62%) out of 21 values follow the equation $y = 100/x$. This means that the frequency y depends on sample size x alone, because only one twin birth is contained in each sample. 5 (24%) of the 21 values follow $y = 0/x$, that is, no twin birth was observed in a sample of x births. Only three values (14%) are independent of both trends. In contrast to this, values

TABLE 6 – Variation of the same twinning frequencies as those in Figure 4, divided in four groups according to sample size.

Group	Sample size (N)	Number of estimates	Twinning frequencies			
			Mean	Range	Variance s^2	Coefficient of variation
1	$N_1 \leq 82$	10	1.81	0-5	2.101	0.800
2	$86 \leq N_2 \leq 305$	10	0.65	0-2.33	0.439	1.024
3	$350 \leq N_3 \leq 937$	10	0.40	0-0.80	0.046	0.537
4	$1003 \leq N_4$	10	0.24	0.09-0.44	0.014	0.496

obtained from larger samples (i.e. more than 500 births, $n = 18$ estimates) seem to be more stable and show a more regular, linear pattern ($r = -0.49$, $p < 0.03$).

If all twinning frequencies for Old World monkeys are ranked by sample size and divided into four equal groups, mean value, range and variance of twinning frequency can in fact be seen to diminish with increasing sample size, that is, from one group to the next (see Table 6). The difference in variance is statistically significant between all combinations of the groups with the F-test (e.g. comparison of groups 1-2: $p < 0.025$, 2-3: $p < 0.005$, 3-4: $p < 0.05$). However, the F-test is very sensitive to scores which are not drawn from a normally distributed population. With the nonparametric Kolmogorov-Smirnov two-sample test, significant differences in the distributions were found only when comparing the groups 1-3 and 1-4 ($p < 0.05$).

Hence, twinning frequencies from the publications here consulted seem to be strongly influenced by the sample size, especially with samples of less than about 500 births, as appears from Figure 4. Such twinning frequencies are obviously not very useful. However, the influence of the sample size decreases with larger samples, and may be neglected if sample size exceeds a certain threshold. For the purposes of this study, an arbitrary limit was set at 1500 births, and twinning frequencies taken from smaller samples were rejected. Thus, only four independent estimates remain; they are listed in Table 7. The estimates range between 0.19 and 0.35 and thus slightly overlap with the lower limit of the twin frequency range in humans (see above). Whereas the combined sample for *Macaca mulatta* does not differ significantly from that of *Papio hamathyas* (Chi-square test, $df = 1$, $0.30 < p < 0.40$), each of the four samples in Table 7 contains significantly fewer twin sets than each the «white» and the «colored» U.S. population samples reported in STRANDSKOV (1945) (Chi-square test, $p < 0.001$).

If the relatively low frequencies in Table 7 are indeed somewhat more realistic estimates than the (usually higher) frequencies derived from the smaller samples, this would contradict the conclusion set forth in a study by WILDT and DUKELOW (1974), who tried to determine which species of the Old World monkeys would most likely be utilized as models for multiple births in humans. The authors suggested that «the baboon, cynomolgus, and bonnet monkeys (*M. radiata*) would be excluded due to the low incidence of twinning observed in the records to date. Finally, based on the data known, it could be concluded that rhesus monkeys (0.5-1.0% twinning) or, more ideally, stump-tailed monkeys (1.2%) would represent most closely the human incidence of multiple births» (WILDT & DUKELOW, 1974, p. 17; see also PASZTOR & VAN HORN, 1979).

It should be noted, however, that for exactly the same two rhesus colonies which

TABLE 7 – *Twinning frequencies in Old World monkeys estimated from four independent samples larger than 1500 births. Some other estimates based on samples of similar size have not been included here, as they partially or completely consist of samples which are already included in those of this list:*

*COURTNEY & VALERIO, 1968 (2 twin sets in 1500 births of *Macaca mulatta*) is contained in VALERIO et al., 1969, this table.*

*WILDT & DUKELOW, 1974 (6 sets in 1567 births of *Papio spp.*) is based on two samples, one of which (LAPIN & YAKOVLEVA, 1963) is contained in ASANOW & LIPPERT, 1976, this table.*

*KOFORD et al., 1966 (4 sets in 1748 births of *M. mulatta*) has not been included, as it combines two different samples, neither of which reach the critical size used here.*

Species	References	No. of twin sets	No. of births	Estimated twinning frequency
<i>Macaca mulatta</i>	VALERIO et al., 1969	3	1561	0.19
	PASZTOR & VAN HORN, 1979	5	2000	0.25
	SCHRIER & POVAR, 1984	5	2000	0.25
<i>Papio hamadryas</i>	ASANOW & LIPPERT, 1976	7	2000	0.35
Total		20	7561	0.26

yielded these high frequencies (LAPIN & YAKOVLEVA, 1963, and VAN WAGENEN & ASLING, 1964) much lower frequencies were reported later, when more births had become available (ASANOW & LIPPERT, 1976, and VAN WAGENEN, 1968a, 1972, respectively). A similar trend can also be observed with the small sample of births in the stumptail macaque (*Macaca arctoides*) available to WILDT and DUKELOW (n = 82 births, HENDRICKX & NELSON, 1971), as compared with the much larger sample collected by SCHRIER and POVAR (1984) (see legend to *Figure 4*).

8.2 Hominoidea

The data published so far on the twinning frequency in hominoid species are even less conclusive. Estimates for the twinning frequency of the chimpanzee range from 1 to 5%. The lowest rate, reported by BREITINGER (1951), is based on one twin set in about 100 births of the chimpanzee colony at the Yerkes Laboratories (Anthropoid Experiment Station of the Yale University, Florida, now at the Yerkes Regional Primate Research Center). The highest rate was reported by PEACOCK and ROGERS (1959) for the same chimpanzee colony (six sets of twins born in 120 parturitions). These authors were the first to suggest that the twinning rate in this species may be higher than that in humans, a possibility that has been repeatedly emphasized (KEELING & ROBERTS, 1972; MARTIN, 1981; SCHULTZ, 1969)¹.

This suggestion should, however, be handled carefully, as the following conditions may have restricted the significance of the estimated twinning frequencies:

Almost all published estimates of twinning frequency in chimpanzees are based on

¹ PASZTOR and VAN HORN (1976, 1979) reported that the opposite was true, namely that twinning is rarer in the great apes than in humans. However, I have been unable to establish the basis for this claim.

the colony at the Yerkes Regional Primate Research Center (BOURNE *et al.*, 1975; BREITINGER, 1951; GUILLOUD, 1969; MARTIN, 1981; NADLER, cited in GOODALL, 1983). An independent sample was provided by GOODALL (1986): In a community of free living chimpanzees, 59 recorded pregnancies resulting in live births included one set of twins. The twinning rates reported by SCHULTZ (1948) and NESTURKH (1959) contain at least in part additional observations on chimpanzee twins: three twin sets in about 100 births and two sets in about 75 births, respectively.

– Four males and 7 females contributed to the 11 sets of twins and one set of triplets in the Yerkes colony (NADLER, cited in GOODALL, 1983). Of these 12 sets, 8 were sired by one male, and 5 were delivered by one female (MARTIN, 1981, p. 345).

– The size of the sample, with a total number of 300 births (NADLER, cited in GOODALL, 1983), is still relatively small and far below the critical sample size derived from variability of twinning rate estimates in Old World monkeys (see above).

Just recently, a more adequate sample has become available: SEAL *et al.* (1985) analysed census data from ISIS and estimated a twinning rate of 1.7% (22 sets in 1311 births). These data also include the births at the Yerkes Chimpanzee Colony. The authors suspected that this -twinning rate was «strongly biased by the multiple twin births that occurred in two dams». One female (from the Yerkes Chimpanzee Colony) had produced four sets of twins, another female had produced five sets. By removing such bias, the authors estimated a corrected twinning frequency of 1.1%. Based on this corrected estimate, SEAL *et al.* (1985) concluded that the twinning frequency in chimpanzees is not different from that in humans (assuming a human twinning rate of 1.11%). Reservations regarding the use of the latter twinning frequency as a human standard have already been presented above. Apart from this, the authors unfortunately failed to explain how the removal of the bias in their chimpanzee sample was achieved. In addition, they assume a priori that the bias were introduced by the recurrence of multiple offspring with some females. However, an analysis of the incidence of multiple offspring in the Yerkes Chimpanzee Colony revealed that the recurrence of such offspring to some males is at least as impressive: One male sired 8 out of 17 sets of multiple offspring, and another male is ancestor of 13 of these sets (GEISSMANN, 1990, see also chapter 9).

The available birth samples for other apes are much smaller and may, therefore, be even less reliable:

– Out of a total of 142 conceptions recorded between 1956 and 1980 for the gorilla population in the United States, only one twin birth was reported (MURPHY, 1982). Using data from the international gorilla studbook and from ISIS, SEAL *et al.* (1985) calculated a twinning frequency of about 0.8% (two sets in 246 births) and stated that it was not different from that in humans. As in the chimpanzee, the twinning frequency for the gorilla has previously been reported to be higher than that of humans, based on the evidence of one twin set in 18 births (KIRCHSHOFER, cited in LANG, 1973).

– In 538 captive births recorded in the orang-utan studbook between 1946 and 1978, there were 9 pairs of twins (JONES, 1982). On the basis of data from the international orang-utan studbook and from ISIS, SEAL *et al.* (1985) estimated a twinning frequency of about 1.1% (seven sets in 626 births) and again found that it was not different from that in humans. It is not clear why the second report recognizes two twin sets less than the first one. Again, an earlier smaller sample gave a much higher rate (four twin sets in 170 births: LANG, 1973).

– For the siamang (*Hylobates syndactylus*), SCHMIDT (in press) estimated that a total of 325 births with 5 known sets of twins occurred in zoos between 1962 and 1986.

8.3 Monozygotic and dizygotic twinning rates

Based on the evidence to date, even a most preliminary estimation of the rate of monozygotic (MZ) and of dizygotic (DZ) twins from the total number of maternities can, therefore, only be attempted for the cercopithecoid sample (consisting mainly of data on macaques and baboons), but not for the nonhuman hominoid sample. In practice, the figures for monozygotic and dizygotic twinning rates are often expressed as rates per thousand maternities. From the cercopithecoid estimates of twinning frequency, ranging from 0.19 to 0.35 sets of twins in a total of 100 births (*Table 7*), and from the proportion of monozygotic twins, ranging from 34.0 to 34.6% of all twins (*Table 3*), I calculate a monozygotic twinning rate of 0.6 to 1.2 sets per thousand maternities, and a dizygotic rate of 1.2 to 2.3‰.

For human populations, it is generally believed «that in reliable data the dizygotic twinning rate may vary widely under different circumstances but that the monozygotic twinning rate is remarkably constant» (BuLMER, 1970, p. 74), and that «in all the races investigated, the rate of MZ pairs of twins calculated by Weinberg's method is about 3-5‰ of the total maternities» (ERIKSSON, 1973, p. 16), while the wide inter-population variations in the DZ twinning rate result in a range from about 2 to 52‰ (ERIKSSON, 1973, p. 17, see also EDWARDS, 1977b). Based on available data, it would seem that both the preliminary monozygotic and the dizygotic twinning rates of Old World monkeys range at, or perhaps even below, the lower limit of the respective ranges in human populations.

Possible influences on twinning rate

It is generally believed that causal relationships exist between the occurrence of human twins and hereditary factors (e.g. BULMER, 1960; CARMELLI *et al.*, 1981; GREULICH, 1934; KHOURY & ERICKSON, 1983; PARISI *et al.*, 1983; SCHMIDT *et al.*, 1983; Stengel, 1980; VOGEL, 1961; WATERHOUSE, 1950; WYSHAK & WHITE, 1965), but the data on the inheritance of a tendency toward twinning seem to be largely inconclusive and the genetic details remain unclear (e.g. CAVALLI-SFORZA & BODMER, 1971; LENZ, 1964; SCHMIDT *et al.*, 1983). The published evidence on the inheritance of twinning in man has been reviewed by BULMER (1970) and, in more detail, by ERIKSSON (1973).

It is possible that a genetic mechanism is operating in the etiology of twinning in nonhuman catarrhines, as has been suggested for some strepsirrhine monkeys PASZTOR & VAN HORN, 1976, 1979; VAN HORN & EATON, 1979; see also IZARD & SIMONS, 1986). For colonies with a high amount of inbreeding, the presence of twin-prone animals may then lead to unusually high twinning frequencies. A similar 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 (ERIKSSON, 1962, 1973; ERIKSSON *et al.*, 1976, 1980). Elevated twinning frequencies have also been recorded in other relatively isolated and endogamous human populations (CARMELLI *et al.*, 1981; SCHMIDT *et al.*, 1983), and in individual family lines (e.g. GEDDA, 1951; PARISI *et al.*, 1983; SHEETS, 1984).

In Old World monkeys, repeated births of twins with the same mother or the same father (ASANOW & LIPPERT, 1976; COURTNEY & VALERIO, 1968; VALERIO *et al.*, 1969) and the occurrence of twin births in related individuals (ASANOW & LIPPERT, 1976) have been reported for some colonies, whereas in others, all twins were from different family lines (VAN WAGENEN, 1972; GAREY *et al.*, 1985). MOHNOT & MOHNOT (1982) recorded four twin births in free-ranging Hanuman langurs (*Presbytis entellus*), three of which were from mothers who belonged to the same maternal stock in one band. The remaining twin birth was observed in a distant group. A striking recurrence of multiple births has also been reported in three colonies of chimpanzees:

– 19 successful pregnancies at the Washington Park Zoo in Portland, Oregon, produced at least three sets of twins, all born to the same female and sired (as were all her babies) by the same male (YEUTTER, personal communication cited in GOODALL, 1983, and 1986).

– One female at Norman (University of Oklahoma) produced five sets of twins (SEAL *et al.*, 1985).

– Of 304 deliveries at the Yerkes Regional Primate Research Center, Atlanta, 11 sets of twins and one set of triplets have been recorded (see above). One male was reported to account for the siring of the great majority, 8 out of 12 sets, and one female for the delivery of 5 of the 12 sets (MARTIN, 1981; NADLER, cited in GOODALL, 1983; see also BOURNE, 1967). Additional twin births have occurred since these reports (see below).

However, even if the accumulation of multiple births in pedigrees was not purely fortuitous, it should be noted that neither the existence of twin-prone animals nor the recurrence of multiple births to related animals provides, by itself, conclusive evidence for a relationship between genetical factors and twinning, as non-genetic factors (environmental causes) could also account for these observations.

GEISSMANN (1990) describes the incidence of multiple births in the Yerkes Chimpanzee Colony in more detail and presents pedigree charts for all (16 sets of twins, 1 set of triplets), revealing that:

1) only a few males (9) and a few females (12) in the colony produced multiple offspring,

2) some males (2) and some females (2) have produced more than one set of multiple offspring,

3) only a few males and a few females are ancestors of multiple births; for instance, one male (Jack) is ancestor to 13 of the 17 sets (see *Figure 5*),

4) female twins (2) themselves produced twins.

These observations indicate that the incidence of multiple births may be a family trait and suggest that this characteristic may be genetically influenced in this chimpanzee colony. A relatively high level of inbreeding may have enhanced the incidence of multiple births in these family lines: The mean inbreeding coefficient for the 17 multiple births was 0.0152 (GEISSMANN, 1990), while the mean inbreeding coefficient for all chimpanzees in the colony was reported to be 0.0079 (ECKHARDT, 1982).

It has been suggested that twinning tendency in man is associated with high gonadotropin levels (e.g. MARTIN *et al.*, 1984; MILHAM, 1964; NYLANDER, 1973, 1978). Artificial induction of ovulation can be accomplished by treatment with gonadotropins (e.g. GEMZELL, 1962). This is of clinical importance as a common therapeutic treatment for women who are anovulatory. Regimes currently in use to induce ovulation include for instance pituitary follicle-stimulating hormone (FSH), human chorionic gonadotropin (HCG), human menopausal gonadotropin (HMG), and others. The drug Clomiphene, which may induce LH release through action on the hypothalamus, has also been widely used. However, the responses of individual patients vary considerably and many of the more hormone-sensitive patients tend to over-react with very high multiple ovulation and undesirable degrees of multiple pregnancy, various degrees of ovarian overstimulation (known as the hyperstimulation syndrome), and a relatively high pregnancy wastage (e.g. AUSTIN, 1975; EDWARDS, 1977a; HACK & LUNENFELD, 1979; WYSHAK, 1978).

Treatment with gonadotropins is in common use for inducing ovulation in domestic and laboratory animals, and it is known that the number of ovulations can be raised over the normal level with an increase of the dose (POLGE, 1977).

Hormonal induction of ovulation with gonadotropins in several species of New and Old World monkeys has been reported to result in multiple ovulations (BENNETT, 1967; BRECKWOLDT *et al.*, 1971; CATCHPOLE & VAN WAGENEN, 1975; DUKELOW, 1970, 1979, 1983; DUKELOW *et al.*, 1972; JAINUDEEN & HAFEZ, 1973; KUEHL & DUKELOW, 1975; MAHONEY, 1975; OSHIMA, 1980; SIMPSON & VAN WAGENEN, 1958, 1962; VAN WAGENEN,

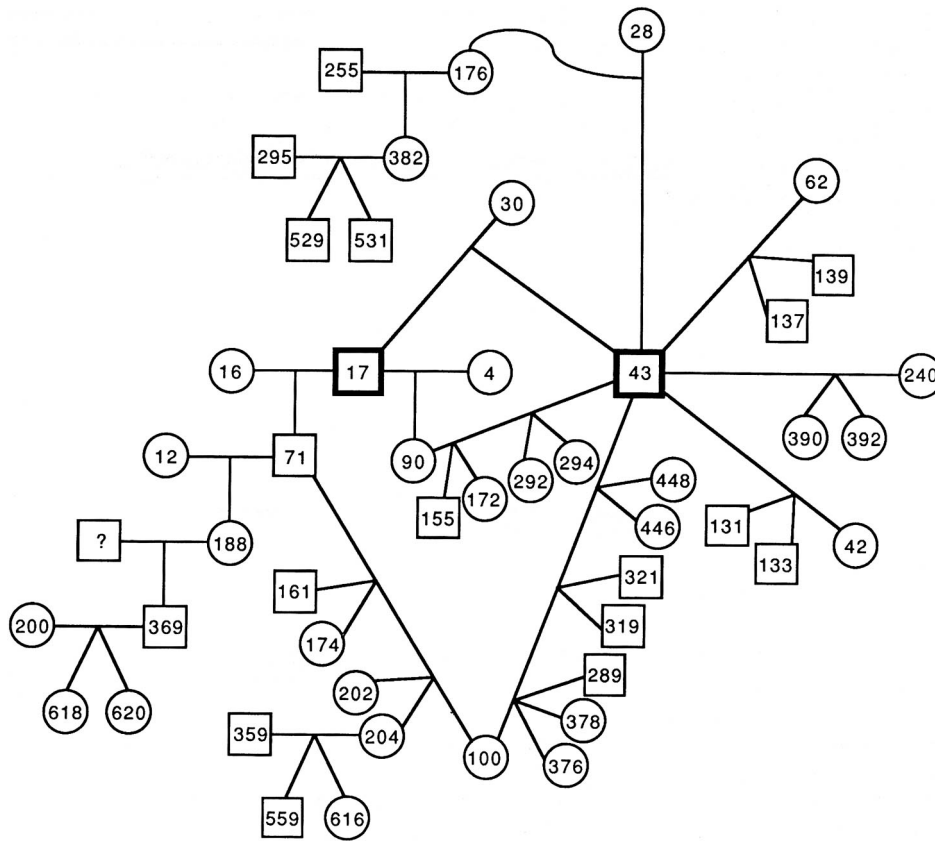


Figure 5. – Pedigree chart of one Yerkes chimpanzee male («Jack», number 17) that is ancestor of 13 sets of multiple births. One of his sons («Hal», number 43) is ancestor of 9 and father of 8 of these sets. Males are symbolized by squares and females by circles. Only family lines ending in multiple offspring are shown.

1968b; VAN WAGENEN & SIMPSON, 1957a, b), and it has been suggested that treated females in macaque colonies would in future furnish litters of three or more infants (VAN WAGENEN, 1968a). Nevertheless, the development of a refractory state after some courses of treatment (ROUSSELL *et al.*, 1968), effects of overstimulation (AUSTIN, 1972), the observation that a large proportion of the oocytes in the enlarged ovaries were clearly abnormal (ROUSSELL *et al.*, 1968), and other observed anomalies of the ovulatory mechanisms (JAINUDEEN & HAFEZ, 1973) would all appear to represent serious objections to the induction of multiple ovulation in simians (AUSTIN, 1975).

Recently, it has been proposed that diet may provide a further source of exogenous influence on twinning both in man (NYLANDER, 1978) and in rhesus macaques (GAREY *et al.*, 1985). Among the natural plants consumed as food by the free-ranging rhesus monkeys of the Morgan Island, South Carolina breeding colony, the roots of *Smilax bona-nox* were identified. It has been suggested that *S. bona-nox* contained, like other *Smilax* species, steroidal saponin. Injection of *S. bona-nox* ethanol extract as well as injection

of pure steroidal saponin into immature female rats have both produced uterine stimulation. The plant was suggested to be a factor in the twinning observed among the Morgan Island monkeys. However, the four sets of twins in 928 live births of this colony (CAREY *et al.*, 1985; TAUB, 1983) do not necessarily indicate an elevated twinning rate and these values are not outside of the range of other samples of similar size (see *Figure 4*). The comparison with each of the rates in *Table 7* does not suggest a significant difference (Fisher exact probability tests, $p \geq 0.33$ with each comparison).

Summary and conclusions

1. This survey of the literature covers a total of 178 reported cases of multiple births, from representatives of 28 species of nonhuman catarrhine primates. This number includes four sets of triple births and two double monsters. The present list of multiple births (*Table 1*) largely extends the number of known cases and more than doubles the number of species with confirmed cases of twinning as compared to earlier reports (e.g. SCHULTZ, 1948, 1956),

2. The known cases of twinning are not evenly distributed among the species of catarrhine primates. Forms which are most numerous in nature as well as in collections and which seem to breed most readily in captivity seem to be overrepresented in the reports to date: rhesus macques (*Macaca mulatta*) and hamadryas baboons (*Papio hamadryas*) contribute 41% of the births known for the cercopithecoid monkeys, whereas chimpanzees (*Pan troglodytes*) contribute 60% to the multiple births known for hominoids. Observation of multiple births in many, if not all catarrhine species may therefore be largely a question of sample size.

3. In the literature, examination of zygosity has been reported of only 19.4% (12 of 62) of all sets of same-sexed twins. Therefore, the difference method and the method of maximum likelihood have been applied to gain rough estimates for the proportion of monozygotic twins in the total number of twin births. The estimate for Old World monkeys with the difference method (34.6% or 18 of 52 sets) seems to be higher than that for apes (25.6% or 11 of 43 sets), but the difference is not statistically significant. The tentative nature of these estimates is stressed.

4. Although a high perinatal mortality rate of twins in captive Old World monkeys and apes was found repeatedly mentioned in the literature, it has not been demonstrated that perinatal mortality is higher in twins than in single-born infants (with one exception: SEAL *et al.*, 1985). No clear evidence in support of this assumption could be drawn from the published data on Old World monkeys. Only the data available for chimpanzees suggest that the rate of abortions and stillbirths may actually be higher in twins than in singletons. The difference is statistically significant both for the ISIS data used by SEAL *et al.* (1985) and for the data from the Yerkes Chimpanzee Colony taken alone. The combined sample of catarrhine twins also shows an excess of abortions and stillbirths in pairs of like sex, as compared to the rate in pairs of unlike sex (Chi-square test, $df = 1$, $0.025 < p < 0.05$). A similar result has been obtained for human twin births.

5. While several reports stress the rearing difficulties experienced by mothers of twins, several sets of twins in catarrhine monkeys and apes have been successfully reared by their own mothers, both in captivity and in nature. The way mothers react to twin offspring also seems to be very variable. It is not clear from the reports consulted whether an attempt to rear twins is in fact disadvantageous for the reproductive success of a mother as compared with raising two single offspring separately. A certain consistency in finding mothers preferring one infant of a set of twins while being to some degree reluctant to accept the other infant and to care for it may point to a behaviour possibly inherent to the maternal affectional system of macaques and eventually other catarrhines. Other rearing complications, which are related to the multiple infant situation, may derive from the following recurrent situations:

- inability of the mother to provide sufficient milk for multiple offspring,
- developmental differences between multiple offspring,
- initial difficulty in establishing secure ventral clinging by more than one infant at the same time.

Each of these situations may at least partially be responsible for the ambivalence which mothers display toward their multiple infants and for their repeatedly reported preference for one of them.

SAVAGE and SNOWDON (1982) suggested that a mother may under certain circumstances improve the chances of survival for a least one of her twin offspring if she abandons the weaker of the two. Apparently, only two such cases have been observed so far, one in rhesus macaques in a laboratory context (DEETS & HARLOW, 1974), and one in feral mountain gorillas (WATTS & HESS, 1988).

6. It has been repeatedly suggested that twinning frequency in most catarrhine primates was approximately the same as in humans, whereas the frequency in the chimpanzee and the gorilla might be higher. It has been demonstrated in this report that most data on twinning frequency in Old World monkeys and apes should not be used because of their small sample size. A lower limit of 1500 births was used here, and all frequency estimates taken from smaller samples were rejected. Thus, only four estimates for *Macaca mulatta* and *Papio hamadryas* remain. The estimates range from 0.19 to 0.35% and are, in fact, lower at least than the frequencies of the U.S. human populations and probably of most (but not necessarily all) human populations.

The published birth samples for apes are, however, relatively small, and the resulting twinning rates may not be reliable. The largest was provided by SEAL *et al.* (1985) for the chimpanzee (22 sets in 1311 births). The reported incidence of twinning in this sample may, however, be biased due to the recurrence of multiple births in some family lines. A correction proposed by SEAL *et al.* (1985) yields a twinning frequency for chimpanzees of 1.1%, but it remains to be demonstrated whether the used correction is appropriate.

The fact, that three of the four known cases of triplet births in catarrhine monkeys occurred in the *chimpanzee*, each case in a different colony, can be considered an indication (however weak) that the frequency of multiple births in this species may emerge as higher than that in some other species (as for instance the rhesus macaque or the hamadryas baboon) when larger birth samples have become available.

It has also been assumed that the incidence of twinning in Old World monkeys varies between species and colonies (see e.g. HENDRICKX & NELSON, 1971), but the present report still fails to find statistical support for this assumption.

7. Preliminary estimates of the rate of monozygotic and of dizygotic twin births from the total number of maternities are presented here, based on the data on Old World monkeys (mainly on macaques and baboons) available to date. The results indicate relatively low frequencies of both types of twins for this sample, as compared to the respective rates in human populations.

8. – Neither the reported existence of twin-prone animals nor the recurrence of multiple births to related animals gives conclusive support to a relationship between hereditary factors and twinning. The familial incidence of multiple births reported for the Yerkes Chimpanzee Colony appears to be the only support to the hypothesis that the incidence of multiple births may be genetically influenced in nonhuman catarrhine primates.

– Multiple ovulations have repeatedly been induced by hormonal treatment of female monkeys with gonadotropins. However, effects of overstimulation and other anomalies still restrict induction of multiple births for breeding purposes.

– The suggested influence of diet on twinning in a macaque colony is found to be inconclusive, as reliable evidence for an elevated twinning rate in this colony is, so far, lacking.

9. It should be noted that our present knowledge on multiple births in nonhuman catarrhine primates is largely based on casual reports. Such data are likely to be subjected to various biases and, therefore, any conclusions and comparisons must remain severely restricted. Almost no data exist which would allow reliable determinations of twinning frequencies, rates of monozygosity, sex proportions, or perinatal risk in multiple births of these primates. Future research could therefore profitably be directed towards carefully documented case histories, and to collection of data for large series of births from primate colonies in zoological gardens and primate centers, and from wild populations.

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Although Old World primates as a rule give birth only to single offspring, multiple births are known to occur. However, they occur only rarely and this may have discouraged detailed research on this topic, with the last comprehensive review dating from 1948. Nevertheless, explicit statements about the frequency, causes and consequences of multiple births in Old World primates have been repeatedly published in the primatological literature.

This monograph reviews and examines published data on multiple births in nonhuman catarrhine primates. This review reveals that:

- most data consist of anecdotal reports,*
- many of the statements are either based on inadequate samples or*
- seem to be derived from supposed (but unsupported) analogies with the human condition.*

Examination of the original data shows that most current concepts concerning multiple births in Old World primates are not supported by available evidence. Nevertheless, certain general principles emerge from this review that may assist future research.

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