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Twinning frequency in catarrhine primates

It has been repeatedly suggested that twinning frequency in most catarrhine primates is approximately the same as in humans, whereas the frequency in the chimpanzee and the gorilla might be higher. This study presents a re-evaluation of the evidence from the pertinent literature. It can be demonstrated 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 pregnancies is suggested here. If all frequency estimates taken from smaller samples are rejected, only four estimates for *Macaca mulatta* and *Papio hamadryas* remain. The estimates range from 0.19 to 0.35% and are in fact lower than the frequencies of most (but necessarily all) human populations. The published birth samples for apes are, however, relatively small, and the resulting twinning rates may not be reliable.

Key words: Twins - Twinning frequency - Multiple births - Primates - Catarrhini.

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. HENDRICKX & NELSON, 1971; SCHULTZ, 1972), but it is known that multiple births do occasionally occur in various catarrhine species. 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). However, the frequency of the phenomenon is still unknown.

The present report, apart from accumulating the previously published evidence, permits some preliminary assessment of current thinking on the frequency of twin births in nonhuman catarrhine primates. This may be of interest, as these simians have been proposed as models for comparative studies on multiple births in man (WILDT & DUKELOW, 1974), and as the occurrence of twin births may influence reproductive success in primate breeding colonies. A comprehensive review of triple births, the zygosity of twin sets, complications of gestation, birth, postnatal development, rearing of multiple offspring, as well as a reassessment of the current hypothesis regarding the occurrence, causes, and consequences of multiple births in nonhuman catarrhine primates, has appeared in a small monograph entitled MULTIPLE BIRTHS IN CATARRHINE MONKEYS AND APES (GEISSMANN, 1989).

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Methods

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 CAVALLI-SFORZA (1980); for the significance thresholds of the F- and the Chi-square-distribution the tables of CIBA-GEIGY (1980) are used.

Twinning in catarthines

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 frequency of plural births in humans was thought to be somewhere between 1.1 and 1.3%, 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 (1968, 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, 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.

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 (RAWLINS *et al.*, 1984) to 0.51% (VAN WAGENEN, 1972), or in *Papio hamadryas* from 0.35 (ASANOW & LIPPERT, 1976) to 1.67% (ABEL, 1933).

Figure 1 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 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 1*). 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 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 1*). 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 1*. 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 paper, an

TABLE 1 - *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

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 2*. 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 hamadrya*s (Chi-square test, df = 1, 0.30 < p <0.40), each of the four samples in Table 2 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 2* 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, stumptailed 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 yielded these high frequencies (LAPIN & YAKOVLEVA, 1963, and VAN WAGENEN & AS-

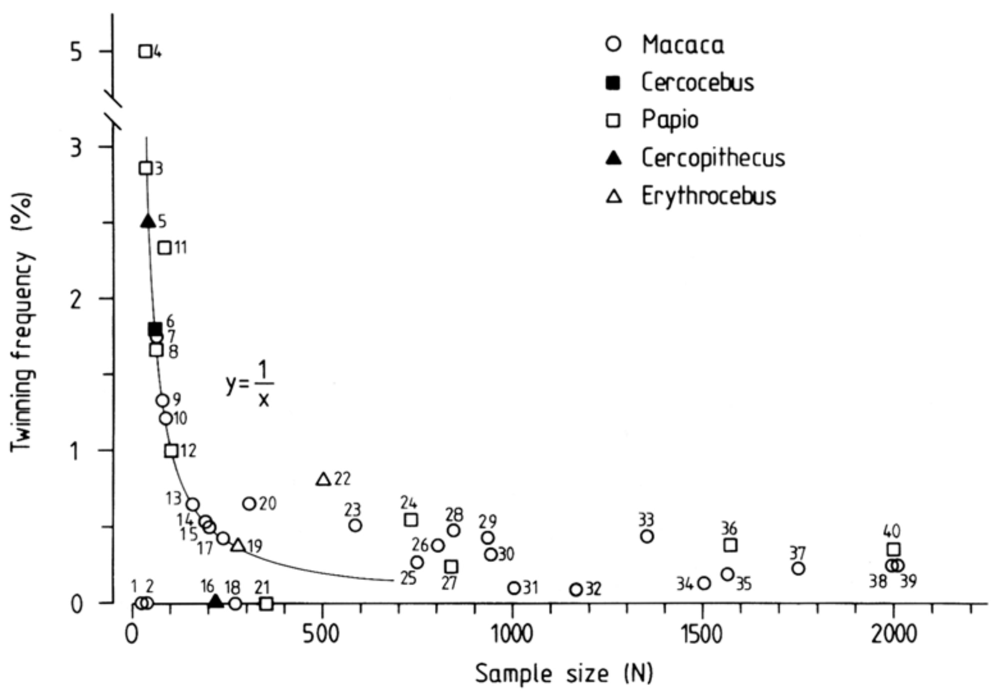

Figure 1. – Interdependence between sample size and twinning frequency in cercopithecoids.
The list (see facing page) gives the source of each sample, the numbers in the figure correspond to the sample number in the list. Only samples of more than 20 births were used.

LING, 1964) much lower frequencies were reported later, when more births had become available (ASANOW & LIPPERT, 1976, and VAN WAGENEN, 1968, 1972, respectively). A similar trend can also be observed with the small sample of births in the stumptail macaque 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 1).

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

Legend to Figure 1 (continued)

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

TABLE 2 - *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.*
WILD & 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
Macaca mulatta	VALERIO *et al.*, 1969	3	1561	0.19
	PASZTOR & VAN HORN, 1979	5	2000	0.25
	SCHRIER & POVAR, 1984	5	2000	0.25
Papio hamadryas	ASANOW & LIPPERT, 1976	7	2000	0.35
Total		20	7561	0.26

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 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

[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.

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 occured 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 was 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).

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.

Summary and conclusions

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 hamadyas* 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 (see GEISSMANN, 1989), 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.

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References

ABEL W., 1933. *Zwillinge bei Mantelpavianen und die Zwillingsanlage innerhalb der Primaten.* Zeitschrift für Morphologie und Anthropologie, 31: 266-275.

ANONYMOUS, 1972. *Twin chimps saved by Cesarean.* Yerkes Newsletter, 9 (2): 18.

ASANOW N.S. & LIPPERT W., 1976. *Bemerkungen zum Verhalten einer Mantelpavian-Gruppe (*Papio hamadryas*) gegenüber einer Mutter mit Zwillingen.* Der Zoologische Garten (NF), 46: 108-117.

BOURNE G.H., KEELING M.E. & BOURNE M.N.G., 1975. *Breeding anthropoid apes and rhesus monkeys at the Yerkes Primate Center.* In (F.T. Perkins and P.N. O'Donoghue, P.N., eds.). Breeding simians for developmental biology. Laboratory Animal Handbooks 6: 63.76. London: Laboratory Animals Ltd.

BREITINGER E., 1951. *Schimpansenzwillinge. Die Mehrfrüchtigkeit bei den Primaten.* Die Umschau in Wissenschaft und Technik, 51: 563.565.

BRÜGGEMANN S. & GRAUWILER J., 1972. *Breeding results from an experimental colony of* Macaca arctoides. In (El. Goldsmith and J. Moor-Jankowski, eds.). Medical primatology 1972, part 1: General primato, logy, reproduction and perinatal studies, genetics, phylogenetics and evolution, pp. 216.226. Basel: Karger.

BULMER M.G., 1970. *The biology of twinning in man.* Oxford: Clarendon Press.

BURTON F.D. & de Pelham A., 1979. *A twinning event in* Macaca sylvanus *of Gibraltar.* Journal of Medical Primatology, 8: 105-112.

BURTON F.D. & Sawchuk L.A., 1974. *Demography of* Macaca sylvanus *of Gibraltar.* Primates, 15: 271-278.

CAVALLI-SFORZA L.L., 1980. *Biometrie. Grundzuge biologisch-medizinischer Statistik.* Stuttgart: Fischer (5th ed.).

CIBA-GEIGY, 1980. *Wissenschaftliche Tabellen Geigy, Teilband Statistik.* 8th ed. Easel: Ciba.Geigy.

COURTNEY K.D. & Valerio D.A., 1968. *Teratology in* Macaca mulatta. Teratology 1: 163-172.

ERIKSSON A.W., 1973. *Human twinning in and around the Åland Islands.* Commentationes Biologicae, 64: 1-159. Helsinki, Finnland: Societas Scientiarum Fennica.

FLEISCHHACKER W., 1968. *Die Frankfurter Gorilla-Zwillinge.* Anthropologischer Anzeiger, 31: 55-69.

GAREY J.D., ERB MEULI L., BEERS W.H., HOLDEN M. & JOLLY C.J., 1985. *Diet and twinning in rhesus monkeys.* American Journal of Primatology, 8: 338.339 (Abstract only).

GEISSMANN T., 1989. *Multiple births in catarrhine monkeys and apes – A review.* Firenze: Il Sedicesimo.

GEISSMANN T., 1990. *Familial incidence of multiple births in a colony of chimpanzees (*Pan troglodytes*).* Journal of Medical Primatology, 19 (in press).

GOODALL J., 1983. *Population dynamics during a 15 year period in one community of free-living chimpanzees in the Gombe National Park, Tanzania.* Zeitschrift für Tierpsychologie, 61: 1-60.

GOODALL J., 1986. *The chimpanzees of Gombe. Patterns of behavior.* Cambridge: Belknap Press.
GUILLOUD N.B., 1969. *The breeding of apes: Experience at the Yerkes Regional Primate Research Center and a brief review of the literature.* Annals of the New York Academy of Sciences, 162: 297-300.
GUTTMACHER A.F., 1953. *The incidence of multiple births in man and some of the other Unipara.* Obstetrics and Gynecology, 2: 22-35.
HARMS J.W., 1956. *Fortpflanzungsbiologie.* In (H. Hofer, A.H. Schultz and D. Starck, eds.). Primatologia. Handbuch der Primatenkunde, Vol. I: Systematik, Phylogenie, Ontogenie, pp. 561-660. Basel: Karger.
HENDRICKX A.G., HOUSTON M.L. & KRAEMER D.C., 1968. *Observations on twin baboon embryos (*Papio *sp.).* Anatomical Record, 160: 181-186.
HENDRICKX A.G. & NELSON G., 1971. *Reproductive failure.* In (E.S.E. Hafez, ed.). Comparative reproduction of nonhuman primates, pp. 403-425. Springfield, Ill.: Thomas.
HEUSER R.L., 1967. *Multiple births: United States – 1964.* U.S. Public Health Service. Publication No. 1000, set. 21, no. 14, 50 pp. Washington: National Center for Health Statistics.
HILL W.C.O., 1970. *Primates. Comparative anatomy and taxonomy. 8. Cynopithecinae:* Papio, Mandrillus, Theropithecus. Edinburgh: Edinburgh University Press.
JONES M.L., 1982. *The orang utan in captivity.* In (L.E.M. DeBoer, ed.). The orang utan. Its biology and conservation, pp. 17-37. The Hague: Dr. W. Junk Publishers.
KEELING M.E. & ROBERTS J.R., 1972. *Breeding and reproduction of chimpanzees.* In (G.H. Bourne, ed.). The chimpanzee, Vol. 5: 127-152. Basel: Karger.
KHOURY M.J. & ERICKSON J.D., 1983. *Maternal factors in dizygotic twinning: evidence from interracial crosses.* Annals of Human Biology, 10: 409-416.
KOFORD C.B., FARBER P.A. & WINDLE W.F., 1966. *Twins and teratisms in rhesus monkeys.* Folia Primatologica, 4: 221-226.
KUSHNER H., KRAFT-SCHREYER N., ANGELAKOS E.T. & WUDARSKI E.M., 1982. *Analysis of reproductive data in a colony of African green monkeys.* Journal of Medical Primatology, 11: 77-84.
LANG E.M., 1973. *Zwillinge bei unsern Orang-Utans.* Zolli (Bull. Zool. Garten, Basel), 31: 14-15.
LAPIN B.A. & YAKOVLEVA L.A., (1963). *Comparative pathology in monkeys.* (U. S. Joint Publications Research Service, transl.). Springfield, Ill.: Thomas.
MARTIN D.E., 1981. *Breeding great apes in captivity.* In (G.E. Graham, ed.). Reproductive biology of the great apes. Comparative and biomedical perspectives, pp. 343-373. New York: Academic Press.
MOSTELLER M., TOWNSEND J.I., COREY L.A. & NANCE W.E., 1981. *Twinning rates in Virginia: Secular trends and the effects of maternal age and parity.* In (L. Gedda, P. Parisi and W.E. Nance, eds.). Twin research 3. Part A: Twin biology and multiple pregnancy, pp. 57-69. Progress in clinical and biological research, 69A. New York: Alan R. Liss.
MURPHY M.F., 1982. *Breeding statistics of western lowland gorillas* Gorilla g. gorilla *in the United States Zoological Parks.* International Zoo Yearbook, 22: 180-185.
NESTURKH M., 1959. *The origin of man.* Moscow: Foreign Languages Publishing House.
PASZTOR L.M. & VAN HORN R.N., 1976. *Twinning in prosimians.* Journal of Human Evolution, 5: 333-337.
PASZTOR L.M. & VAN HORN R.N., 1979. *Twinning.* In (E.J. Andrews, B.C. Ward and N.H. Altman, eds.). Spontaneous animal models of human disease, Vol. I: 227-230. New York: Academic Press.
PAUL A. & THOMMEN D., 1984a. *Differentieller Reproduktionserfolg und Reproduktionsstrategien weiblicher Berberaffen (*Macaca sylvanus*).* Anthropologischer Anzeiger, 42: 185-190.
PAUL A. & THOMMEN D., 1984b. *Timing of birth, female reproductive success and infant sex ratio in semifreeranging barbary macaques (*Macaca sylvanus*).* Folia Primatologica, 42: 2-16.
PEACOCK L.J. & ROGERS C.M., 1959. *Gestation period and twinning in chimpanzees.* Science, 129: 959.
RAWLINS R.G., KESSLER M.J. & TURNQUIST J.E., 1984. *Reproductive performance, population dynamics and anthropometrics of the free-ranging Cayo Santiago rhesus macaques.* Journal of Medical Primatology, 13: 247-259.
RUDAT K.-D., 1948. *Mitteilung einer Zwillingsgeburt bei Javamakaken (*Macaca irus mordax *Thomas u. Wroughton* Cynomolgus *L.).* Zentralblatt für Gynäkologie, 70: 77-80).
SCHMIDT C.R. (in press): *Twin births in siamang (*Symphalangus syndactylus*).* Int. Zoo News.
SCHRIER A.M. & POVAR M.L., 1984. *Twin stumptailed monkeys born in laboratory.* Laboratory Primate Newsletter, 23 (3): 18.
SCHULTZ A.H., 1948. *The number of young at a birth and the number of nipples in primates.* American Journal of Physical Anthropology (N.S.), 6: 1-23.
SCHULTZ A.H., 1956. *The occurrence and frequency of pathological and teratological conditions and of*

twinning among non-human primates. In (H. Hofer, A.H. Schultz and D. Starck, eds.). Primatologia. Handbuch der Primatenkunde, Vol. I: Systematik, Phylogenie, Ontogenie, pp. 965-1014. Basel: Karger.

SCHULTZ A.H., 1969. *The life of primates*. London: Weidenfeld & Nicolson.

SCHULTZ A.H., 1972. *Developmental abnormalities*. In (R.N.T.-W. Fiennes, ed.). Pathology of simian primates. Part 1: General pathology, pp. 158-189. Basel: Karger.

SEAL U.S., FLESNESS N. & FOOSE T., 1985. *Neonatal and infant mortality in captive-born great apes*. In (G.E. Graham and J.A. Bowen eds.). Clinical management of infant great apes, pp. 193-203. New York: Alan R. Liss. Inc.

SIEGEL S., 1956. *Nonparametric statistics for the behavioral sciences*. London & New York: McGraw-Hill.

SLY D.L., HARBAUGH S.W., LONDON W.T. & RICE J.M., 1983. *Reproductive performance of a laboratory breeding colony of patas monkeys (*Erythrocebus patas*)*. American Journal of Primatology, 4: 23-32.

DE SNOO K., 1942. *Das Problem der Menschwerdung im Lichte der vergleichenden Geburtshilfe*. Jena: Fischer.

STARCK D., 1974. *Die Stellung der Hominiden im Rahmen der Säugetiere*. In (G. Heberer, ed.). Die Evolution der Organismen, Vol. 3: Phylogenie der Hominiden, pp. 1-131. (3rd ed.), Fischer: Stuttgart.

STOTT K., 1946. *Twins in green guenon*. Journal of Mammalogy, 27: 394.

STRANDSKOV H.H., 1945. *Plural birth frequencies in the total, the "white" and the "colored" U.S. populations.* American Journal of Physical Anthropology (N.S.), 3: 49-55.

TANAKA T., TOKUDA K. & KOTERA S., 1970. *Effects of infant loss on the interbirth interval of Japanese monkeys. Primates*, 11: 113-117.

TAUB D.M., 1983. *Twinning among nonhuman primates.* American Journal of Primatology, 4: 357 (Abstract only).

TICKELL S.R., 1864a. *Note on the gibbon of Tenasserim,* Hylobates lar. Journal and Proceedings of the Royal Asiatic Society of Bengal, Calcutta, 33: 196-199.

TICKELL S.R., 1864b. *Note on the gibbon of Tenasserim,* Hylobates lar. Annals and Magazine of Natural History, London, 14: 360-363.

VALERTO D.A., MILLER R.L., INNES J.R.M., COURTNEY K.D., PALLOTA A.J. & GUTTMACHER R.M., 1969. Macaca mulatta. *Management of a laboratory breeding colony*. New York: Academic Press.

VAN WAGENEN G., 1968. *Studies in reproduction (*Macaca mulatta*).* In (C.O. Miller, ed.). Proceedings, Conference on nonhuman primate toxicology, pp. 103-113. Washington: Government Printing Office.

VAN WAGENEN G., 1972. *Vital statistics from a breeding colony. Reproduction and pregnancy outcome in Macaca mulatta.* Journal of Medical Primatology, 1: 3-28.

VAN WAGENEN G. & ASLING C.W., 1964. *Ossification in the fetal monkey (*Macaca mulatta*). Estimation of age and progress of gestation by roentgenography*. American Journal of Anatomy, 114: 107-132.

WILDT D.E. & DUKELOW W.R., 1974. *The nonhuman primate as a model for human twinning.* Laboratory Primate Newsletter, 13 (4): 15-18.

YERKES R.M., 1934. *Multiple births in anthropoid apes.* Science, 79: 430-431.

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