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Effects of Hand-rearing on the Reproductive Success of Western Lowland Gorillas in North America

Sadie Ryan,* Steven D. Thompson, Amber M. Roth,† and Kenneth C. Gold

Department of Conservation and Science, Lincoln Park Zoological Gardens, Chicago, Illinois

This study sought to assess the potential effects of hand-rearing by evaluating the relationships among rearing type and reproductive success in the American Zoo and Aquarium Association's Species Survival Plan® for western lowland gorillas. Our study included data on 697 gorillas: 257 wild-born (WB) and 440 born at zoos or related facilities in North America. We found no significant differences in the number of reproductive zoo-born (ZB) and WB females, but more WB males sired infants than their ZB counterparts. This was influenced by a skew in the number of reproductive years for WB males in the studbook. ZB males showed no difference in infants produced per reproductive year, as compared to WB males, while ZB females produced more infants per reproductive year than did WB females. Mother-reared (MR), ZB females produced more offspring and used more reproductive opportunity than hand-reared (HR) females, whereas rearing had no effect on the reproductive success of ZB males. Moreover, MR and partially hand-reared (PHR) females were more likely to become nurturing mothers themselves. Zoo Biol 21:389–401, 2002. © 2002 Wiley-Liss, Inc.

Key words: Species Survival Plans®; western lowland gorillas; reproductive success; mother-rearing; socialization

*Correspondence to: Sadie Ryan, Division of Insect Biology, 201 Wellman Hall, University of California–Berkeley, Berkeley, CA 94720-3112. E-mail: sjryan@nature.berkeley.edu

†Amber M. Roth's present address is: Wisconsin Department of Natural Resources, 107 Sutliff Avenue, Rhinelander, WI 54501.

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INTRODUCTION

The potentially adverse impacts of maternal and social deprivation on sexual behavior and reproductive success in primates are well documented (e.g., rhesus monkeys [Harlow and Harlow, 1965; Harlow, 1971; Davenport, 1979], chimpanzees [Rogers and Davenport, 1969; King and Mellen, 1994], and lowland gorillas [Meder, 1990, 1992; Beck and Power, 1988]). Individuals raised in isolation or hand-reared by human caregivers often 1) exhibit stereotypies, asociality, and other abnormal behaviors [Erwin and Deni, 1979]; 2) fail to establish appropriate sexual posturing for copulation; or 3) lack social-sexual behavior entirely [Mitchell et al., 1979]. Reports that hand-reared (HR) western lowland gorillas have fewer offspring than individuals raised by their mothers [Beck and Power, 1988; Meder, 1993] have been of particular concern to the American Association of Zoos and Aquariums' (AZA) Species Survival Plan® (SSP®) for western lowland gorillas. If HR individuals are less likely to reproduce than mother-reared (MR) individuals, hand-rearing could compromise the demographic and genetic management tactics that the SSP® uses to ensure the maintenance of a self-sustaining population. This study evaluates the potential effects of rearing experience on the reproductive success of gorillas in North American zoos.

Early in the history of the North American zoo gorilla population, hand-rearing was a common practice (Fig. 1). The fear that mother-rearing put gorilla infants at higher risk of death was substantiated by at least one survey [Satterfield and Kiser, 1981], and with the advent of the western lowland gorilla SSP® in 1982, strong emphasis was placed on socialization with conspecifics of the appropriate ages and genders, under the presumption that this would foster natural social behavior and improve breeding success. The SSP® husbandry manual recommended that the average size of a social group be increased to more closely imitate a natural social group and mating structure [Ogden and Wharton, 1997], and mother-rearing was recommended as the preferred method for rearing infant gorillas [Conway et al., 1985], with the explicit stipulation that "[i]nfants should not be removed for hand-rearing unless there is a significant threat to the health of the mother or infant" [Beck and Power, 1988]. "Care should be taken against the premature removal of infants due to anticipated or perceived maternal incompetence…many gorillas show improvement in maternal care during the first few days of an infant's life" [Dubois, 1997]. Other recommendations included improved social integration techniques [Meder, 1990], rearing with conspecifics [Maple et al., 1977; Reichard et al., 1990; Meder, 1992; King and Mellen, 1994], increased caretaker contact [Maple, 1980], introduction of poor breeders to new potential mates [Reichard et al., 1990], varying group composition [Miller-Schroeder and Paterson, 1989], and increased environmental complexity for adults [Miller-Schroeder and Paterson, 1989] and infants [Maple et al., 1977].

Prior studies have suggested that HR female gorillas have lower reproductive success than either MR or wild-born (WB) gorillas [Beck and Power, 1988; Meder, 1993]. However, these studies had relatively small sample sizes, and pooled some rearing types and birth origins. One potential drawback of these earlier studies was that most zoo-born (ZB) specimens had yet to reach maturity, and thus the data disproportionately favored WB over ZB specimens. More than 10 years later we were able to use a much larger database to investigate the possible effects of four

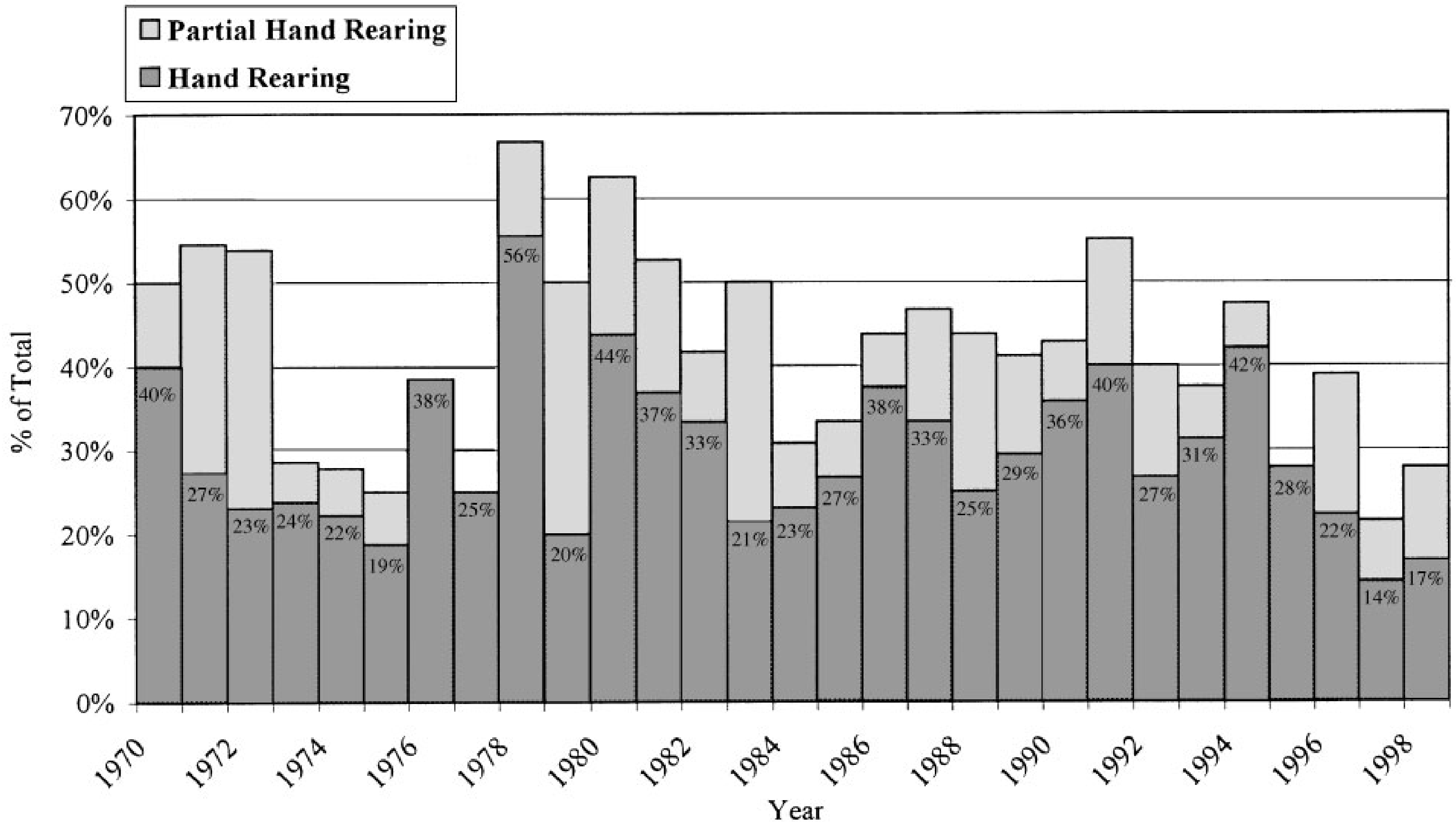

Fig. 1. Proportional frequencies of hand-rearing and partial hand-rearing since 1970.

different rearing situations (HR, partially hand-reared (PHR), MR, and WB) on reproductive success of gorillas in North American zoos. Due to an increased number of specimens and more than 10 additional years of data, our sample represents a nearly threefold increase in reproductive opportunity for captive-born (CB) females over that analyzed by Beck and Power [1988].

METHODS

Data on hand-rearing were extracted from the *North American Studbook of the Western Lowland Gorilla* [Wharton, 1995]. These data were amended and supplemented with data on rearing status obtained by surveys and direct interviews of animal-care and records-keeping staff (Gold, unpublished results). Studbook data were current through February 25 1999, but all analyses of annual bases included data through 1998 only. Data from 1999 were included in analyses when data were pooled across years.

Individuals were classified as MR, HR, PHR, WB, or rearing type unknown. MR gorillas were those that remained with their mother for at least the first 2 years of life. HR gorillas were separated from their mother within 72 hr of birth and cared for by humans until about 2 years of age or older (often younger than 2 in recent years, and usually older than 2 in earlier years). PHR gorillas, as defined by the SSP® and recorded in the studbook, remained with their mother for at least the first 72 hr of life, but were later removed and cared for by humans. They were usually not reintroduced to gorillas until they were about 2 years of age. As the PHR classification includes individuals that may have been mother-reared for almost 2 years, it was not possible to differentiate between infants that spent more time with their mother and those that spent more time with human caretakers. Segregation of the PHR category differs from previous studies that opted to allocate each PHR specimen to either the MR or the HR category.

Gorillas imported from the wild have produced a significant number of offspring in the captive population, and there have been suggestions that WB specimens have enjoyed greater reproductive success than those born in captivity (regardless of rearing experience). However, the type and extent of rearing experienced by virtually all wild- caught gorillas is either unknown or poorly documented. In the absence of specific information, the SSP® assumes that most WB individuals were imported at 1–2 years of age, which would place them in the PHR category. However, to test the hypothesis that some social experience in the wild, presumably within a natural social group, might have significant socialization effects in later life, we placed all wild-born specimens in the rearing category of WB. Because the WB category included a potentially wide range of rearing experiences, we limited analyses of this category to comparisons against all rearing experiences in captivity (i.e., zoo-born).

Since definitions for rearing may be recorded differently outside North America, and accurate historical records were difficult to acquire for individuals that originated outside the SSP®, we excluded all ZB imports from the analyses. Prior studies included ZB individuals from outside North America [Beck and Power, 1988; Meder, 1993].

Analyses of the relationship between the rearing type and reproductive success was limited to sexually mature, ZB individuals (see Table 1). Definitions of "sexually

TABLE 1A. Birth origins and reproductive success

Birth origin	Total in studbook	Adults (age 6+)	Reproductively successful adults	Total RY	Total infants	Inf/RY	%RYU
Males							
Captive born	202	106	22	279.575	87	0.307	0.307
Wild born	122	115	61	1408.255	314	0.241	0.241
Total	324	221	83	1687.83	401	0.259	0.259
Females							
Captive born	206	109	68	837.61	197	0.235	0.536
Wild born	135	120	77	1875.71	253	0.135	0.181
Total	341	229	145	2713.32	450	0.166	0.324

TABLE 1B. Rearing type and reproductive success of captive born gorillas

Birth origin	Total in studbook	Adults (age 6+)	Reproductively successful adults	Total RY	Total infants	Inf/RY	%RYU
Males							
Hand reared	70	55	6	90.12	34	0.389	0.389
Mother reared	77	41	13	165.513	45	0.262	0.262
Partially hand reared	21	10	3	23.942	8	0.339	0.339
Total	168	106	22	279.575	87		
Females							
Hand reared	70	45	24	306.77	61	0.199	0.290
Mother reared	77	40	29	335.42	90	0.268	0.808
Partially hand reared	33	22	15	195.42	46	0.235	0.405
Total	180	107	68	837.61	197	0.235	

mature" for both genders were based on the earliest ages of first reproduction in the North American regional studbook [Wharton, 1995]: 6 years of age (age class 6–7 years) for males and females. Although the studbook contains one record of a male siring an offspring during age class 4–5, the studbook keeper and other husbandry experts consider this datum to be suspect (perhaps a data entry error), as older males were also present at the time of conception. Reproductive success for males was defined as siring an offspring; for females it was a live birth.

A potential bias in evidence of reproductive success is the lack of opportunity to reproduce. This can occur as a result of limited access to potential mates, infertility, or age (e.g., not old enough to have conceived or given birth). Of these potential sources of bias, only age is readily compensated for. For this study, it was assumed that all other individuals were fertile and had access to competent mates for their entire reproductive life. Of course this is an oversimplification, as mate access is governed by the SSP® recommendations and the location of individuals at any point in time. However, the SSP® makes every effort to maintain all mature females in groups containing mature males; while some mature males are maintained without access to mature females (e.g., in bachelor groups), most mature males are eventually housed with mature females. One sterile male (studbook ID 1161) was excluded from all analyses because he had little, if any, opportunity to reproduce before he was sterilized.

To adjust reproductive success for opportunity with respect to age [see Beck and Power, 1988], the number of infants per individual per reproductive year was calculated by dividing the number of live births by the number of years since maturity. The number of reproductive years for each individual was calculated by subtracting the years prior to sexual maturity from the individual's age as of 25 February 1999. For males, the traditional measure of the number of infants divided by the number of reproductive years is an appropriate estimate of used reproductive opportunity.

When the number of infants per year of reproductive opportunity [Beck and Power, 1988] is used as a measure of female reproductive success, females that conceive their first infant before the presumed age of maturity (6 years of age) have used opportunity that exceeds reproductive opportunity. Therefore, many of these individuals have contributed infants to the total, but contributed few years of reproductive opportunity. Mathematically, this problem is further confounded when reproductive opportunity is adjusted to account for time attributable to lactational amenorrhea. Thus, we created a new variable: the "proportion of used reproductive opportunity" (RYU). This measure is defined as the time a female allocates to reproduction (i.e., gestation, the subsequent period of lactational amenorrhea when not cycling, and the interim to first postpartum estrus) relative to the amount of time she was reproductively mature. For this study, the numerator of this ratio is referred to as "reproductive opportunity used" and the denominator as "reproductive opportunity" (as it is measured in years).

To calculate reproductive opportunity used by each female, we summed the number of years devoted to gestation, lactational amenorrhea, and the interim between lactational amenorrhea and first postpartum estrus behavior for each infant born. Gorilla gestation is approximately 0.7 years, and the interim between lactational amenorrhea and first postpartum estrus behavior is approximately 0.2 years [Dixson, 1981]. The median lactational amenorrhea is about 2.4

years for mothers rearing their infants, and near zero for those whose infants are hand-reared [Sievert et al., 1991]. The mean reproductive opportunity used for each MR mother was 3.1 years; for each HR mother it was 0.9 years. Each unknown rearing was assigned the minimum (0.9 years) reproductive opportunity used.

The length of lactational amenorrhea for PHR is more difficult to determine because that category consists of infants who stay with the mother for as little as 3 days to as much as 2 years. Unlike earlier studies [Beck and Power, 1988] (Roth, unpublished results), we had sufficient data to leave the data on hand-rearing vs. mother-rearing unpooled with other data, such as the PHR data. In an earlier study (Roth, unpublished results) the reproductive opportunity used for each PHR mother under varied assumptions were used in separate comparisons for a sensitivity analysis of used reproductive opportunity between the different rearing types. The effects were found not to influence the effects of this rearing type on the overall patterns of effects, so we chose to use an average value for rearing time in the consideration of this variable.

Chi-squared tests were used to analyze the proportions of reproductively successful individuals. Analysis of variance (ANOVA) was used to compare the number of infants per reproductive year and percent of used reproductive opportunity. The multivariate ANOVA (MANOVA) and post-hoc Tukey's honest significant difference (HSD) tests were used to analyze the effects of dam rearing type on offspring rearing. Throughout the analysis, we used a significance tolerance of 0.05; the minimum in any cell was $n = 5$, to maintain the validity of the tests used. All statistical analyses were conducted using the Statistica 99® software package [1984–2001].

RESULTS

The regional studbook database contains information on 710 gorillas. Of the 697 individuals born in or imported to North America, 257 (135 females and 122 males) were WB and 440 (206 females, 202 males, and 32 unknown sex) were ZB (Table 1A). ZB individuals now comprise 63% of the historical North American population. In our analysis of reproductive success and birth origin, there were 257 wild-caught adults (135 females, 121 males, and one sterile male excluded from the analysis) and 349 ZB adults (163 females, 162 males, and 24 of unknown sex). In the analysis of reproductive success due to rearing type, we excluded unknown sex gorillas and those of unknown rearing type.

The proportional frequency of hand-rearing and partial hand-rearing has not declined significantly since the early 1970s (Fig. 1). However, from 1996 through 1998 the frequency of hand-rearing and partial hand-rearing was lower than at any time since 1970 (Fig. 1).

Comparison of Birth Origins

If the reproductive success of ZB and WB individuals is the same, the proportion of reproductively successful females in the populations should be equivalent to the respective proportions of WB and ZB in the total adult female population.

Extrapolating from Table 1A, of 229 adult females, 52.4% were WB and 47.6% CB. Of the 145 reproductively successful (RS) adult females, 53.1% were WB and 46.9% CB; these proportions are not significantly different ($X^2 = 0.02$; $P = 0.8946$). These proportions were different for males: Of 221 adult males, 52% were WB and 48% CB; of the 84 RS males, 73.5% were WB and 26.5% CB ($X^2 = 11.85$; $P = 0.0006$), due to a very skewed distribution of reproductive opportunity (years) between WB and ZB adults (females: 31% CB, 69% WB; males: 17% CB, 83% WB). CB females had higher reproductive success than their WB counterparts in terms of infants per reproductive year (0.23 inf/RY CB vs. 0.13 inf/RY WB: F = 24.04, $P \ll 0.0001$); males had a similar pattern, but this was not significant (0.31 inf/RY CB vs. 0.24 inf/RY WB; F = 1.55; $P = 0.215$).

Comparison of Rearing Types

Of 107 adult CB females, 68 were RS females (Table 1B), although there was a slight tendency for HR females to be less successful (42% of females were HR; 35.3% of HR were successful), and MR females to be more successful (37.4% of females were MR; 42.6% of MR were successful ($X^2 = 3.31$, $P = 0.0687$)). Moreover, neither HR nor MR females differed from PHR females (20.6% PHR, 22.0% PHR of RS (HR: $X^2 = 1.34$, $P = 0.2472$; MR: $X^2 = 0.13$, $P = 0.72$)). Of the 106 adult CB males, only 22 were RS (Table 1B), but proportionally, MR males showed greater reproductive success than HR males. 51.9% of males were HR, of which 10.9% were RS; 38.7% of males were MR, of which 31.7% were RS; ($X^2 = 11.7$, $P = 0.0006$). The proportion of PHR in RS males did not significantly differ from HR and MR males (9.4% PHR, 13.6% PHR of RS (HR: $X^2 = 2.59$, $P = 0.1079$; MR: $X^2 = 0.01$, $P = 0.9169$)).

MR females have had more reproductive opportunity than HR females. RS MR females (n = 29) produced 90 infants during 335.42 years of reproductive opportunity, whereas RS HR females (n = 24) produced 61 infants during 306.77 years of reproductive opportunity. MR males have also had more opportunity to reproduce than HR males. The RS MR males (n = 13) sired 45 infants over 165.513 reproductively opportune years, while RS HR males (n = 6) sired 34 infants during 90.12 years of reproductive opportunity.

In terms of infants/reproductive year (inf/RY), there was a tendency for HR males (HR 0.389 inf/RY, MR 0.262 inf/RY, PHR 0.339 inf/RY) and MR females (HR 0.199 inf/RY, MR 0.268 inf/RY, PHR 0.235 inf/RY) to be more successful than the other rearing types. However, no rearing type created a statistically significant effect (males: HR vs. MR: F = 0.6727, $P = 0.4235$; HR vs. PHR: F = 0.0398, $P = 0.8474$; MR vs. PHR: F = 0.2532, $P = 0.6226$), (females: HR 0.199 inf/RY, MR 0.268 inf/RY, PHR 0.235 inf/RY (HR vs. MR: F = 0.8547, $P = 0.3596$; HR vs. PHR: F = 0.0437, $P = 0.8536$; MR vs. PHR: F = 1.446, $P = 0.2538$)).

To examine reproductive investment of females, we used our measure of percent used reproductive opportunity, or RYU. MR females had a significantly higher reproductive investment than HR females (0.808 RYU vs. 0.290 RYU, respectively; F = 7.381, $P = 0.0089$).

Dam vs. Offspring Rearing

The primary concern in this study was whether the rearing type of females affects the rearing quality of their own offspring. There was a significant effect from the dam's rearing on the rearing type of the offspring (MANOVA: R = 2.99, $P = 0.0091$). Of RS HR dams, 53.7% of their infants were also HR, 31.5% were MR, and 14.8% were PHR. Although this effect on the distribution of infants is not significant, there was a higher number of HR infants being produced by HR dams. Of RS MR dams, 21.3% were HR, 55% were MR, and 23.8% were PHR. There was a significant effect of MR dams producing MR infants (Tukey HSD; $P = 0.043$). Of RS PHR dams, 47.6% of their offspring were HR, 50% were MR, and 2.4% were PHR. WB dams produced offspring that were 42.9% HR, 42.3% MR, and 14.9% PHR.

One institution routinely hand-rears all ZB gorillas, which could bias our analyses of the relationship between a dam's rearing and that of its offspring (i.e., Maple's [1980] "hand-rearing syndrome"). When this institution was removed from the analysis ($n = 35$ zoo births), the proportions of HR dams were affected, with a distribution of 51.1% HR, 31.9% MR, and 17% PHR. Despite the change in proportions, MR dams were the only group with a significant effect on the rearing type of their infants (MANOVA: $R = 2.53$, $P = 0.0238$).

DISCUSSION

Compared to earlier studies, our analyses found fewer differences between the reproductive success of HR and MR gorillas. While many of the differences reported by earlier studies were still present as trends, most were no longer statistically significant and many were diminished in magnitude.

The proportion of ZB adult individuals of both sexes in the population has increased from 50% to 63% since the 1988 study, allowing us to "unpool" the data and examine more closely the effects of rearing types.

Beck and Power [1988] reported that WB females (68%) had greater reproductive success than ZB females (49%). The implication of these results was that, at least through 1988, socialization in captivity might have a negative effect on reproductive success. In contrast, we found that the reproductive success of WB females (62%) and CB females (64%) did not differ significantly (Table 1A). This may be attributable to our larger sample size, increased reproductive opportunity for individuals in our sample, or continuing changes in hand-rearing protocols.

Although Beck and Power [1988] found no difference in reproductive success between WB males (59%) and ZB males (50%), we found that more WB (53%) than ZB (21%) males were reproductively successful (Table 1A). This difference may be attributable to the longevity of WB males and the genetic management strategy of the AZA SSP® programs. Because one SSP® goal is to increase the population's genetic diversity by breeding founders (WB individuals), it is likely that the high priority placed on breeding WB males has, in the short term, relegated many ZB males to nonbreeding situations. It may be at least 10–15 years before ZB males accumulate enough reproductive opportunity to allow subsequent analyses to accurately assess their reproductive success.

Beck and Power [1988] reported a significant difference between the number of infants per reproductive year for ZB males (0.32) and WB males (0.17). We found a similar, albeit not statistically significant, difference between ZB and WB males (Table 1A). Again, the lack of significance here may be due to a genetic management strategy (see above) that favors the placement of WB over ZB in breeding situations.

Our results indicate that more MR females are reproductively successful than HR females (Table 1B; Fig. 2), which is consistent with Beck and Power [1988]. Beck

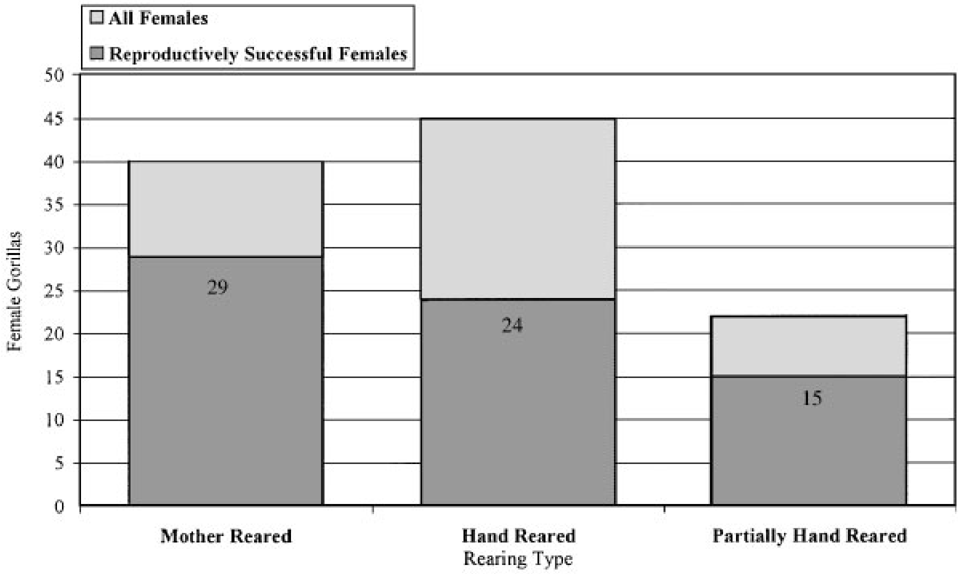

Fig. 2. Number of reproductively successful females and total females by rearing type.

and Power [1988] also found that MR females had a greater number of infants per year of reproductive opportunity (0.30 vs. 0.11); our analyses detected a similar pattern, but it was not statistically significant. However, our analyses show that the proportion of RYU, which we judge to be a more appropriate indicator of maternal success than number of infants born per year of reproductive opportunity, was significantly greater for MR females (45.7%) than HR females (29.4%). For males, rearing type played a significant role in reproductive success, with MR males being more likely to breed than the other rearing types. However, we found that the degree of reproductive success was skewed toward HR males. Although this wasn't a statistically significant result, it was somewhat surprising. One can see from the data that only a few males are having many offspring. The fact that they are hand-reared can be discounted in situations such as artificial insemination, which has been used, albeit rarely, in this SSP® in the last decade. In that instance, the social habits or learning of the male becomes irrelevant, and even his presence is unnecessary for conception to take place. However, hand-rearing may have no negative reproductive effect on male gorillas. The role that partial hand-rearing plays in this study is somewhat vague, due to the vague nature of the category. We suspect most PHR infants were removed from their mother at a fairly young age, probably prior to socialization with conspecifics (3 months at the earliest, according to Fossey, 1982). Therefore, most PHR infants probably spent more of their formative early years with human caretakers than with their mothers and conspecifics. This category represents a compromise between two situations: depriving the infant of early social learning and proper socialization, or leaving the infant with the mother long enough to have that initial bonding. Earlier studies tended either to compare this category to WB infants (Roth, unpublished results), as it was seen to be a partial mother-rearing situation, or to make it a partial-valued category for mother-rearing. This allowed the researchers to pool or lump the datasets together for analyses. This was not done in the present study, as we had the luxury of sufficiently sized datasets. Because we were unable to determine how long PHR individuals were away from the group, quantification of the degree to which it could be seen as beneficial or detrimental was difficult. Having established the baseline data for the effects of rearing in the two extreme categories, the door is open to more extensive and detailed studies of the effects of PHR. To facilitate future investigations into the impacts and trends of hand-rearing, the PHR status could be subdivided into major physical and social developmental stages, or labeled by the month in which the individual was removed from its mother.

Rearing of Dam vs. Infant-Rearing Needs

As one of the major purposes of an SSP is to create and maintain self-sustaining populations, it is important to know whether the rearing environment and reproductive success are affected by the rearing type of the dam. It is encouraging that while it seemed that rearing type was having an effect on the distribution of rearing types of infants produced (Fig. 3), the only significant effect is that MR dams are more likely to rear their offspring; HR and PHR dams are just as likely to rear, or not rear their offspring.

Impact of Gorilla SSP® Recommendations on Hand-Rearing and Reproductive Success

Despite SSP® recommendations, the frequencies of hand-rearing and partial hand-rearing did not decline substantially from the early 1970s through the early 1990s (Fig. 1). Since 1985, 2 years after the formation of the SSP® (and time enough for SSP® recommendations to begin taking effect), over 40% of all CB individuals that lived over 1 year have been hand-reared. However, it is encouraging that since the publication of the husbandry manual [Ogden and Wharton, 1997] and the

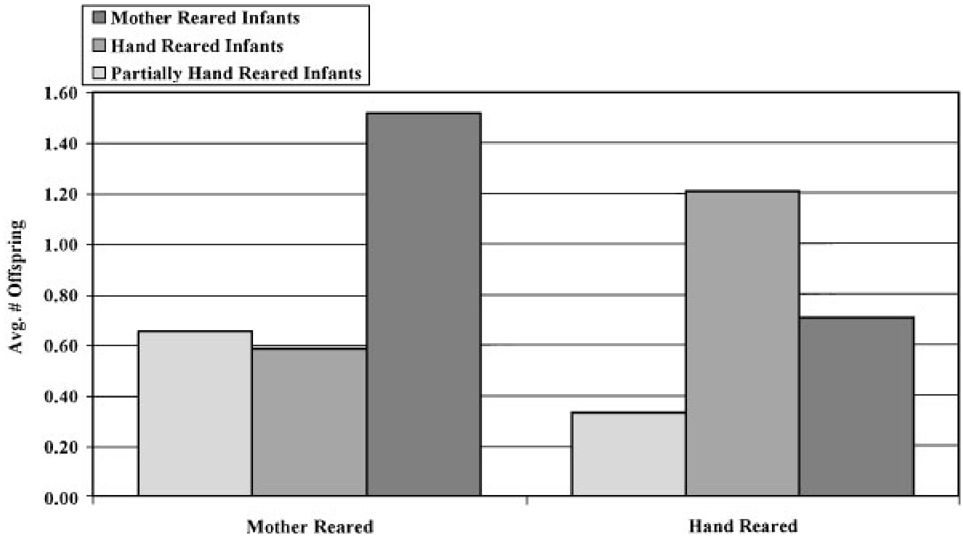

Fig. 3. Rearing type of infants per rearing type of dam.

broader use of protocols to distinguish true maternal neglect from post-partum adjustment, the frequency of hand-rearing has declined substantially.

Other Factors Contributing to Reduction of Reproductive Success or Reproductive Failure

The interaction of hand-rearing with other factors that affect gorilla breeding success may add impetus to its recommended reduction. Abnormal social-sexual behavior, causing reproductive failure in many individuals, is often attributed to hand-rearing. Cases of reproductive failure not due to abnormal social-sexual behavior caused by hand-rearing, such as medical problems and lack of mate access, should be identified and removed from this study.

The variation in breeding success of HR individuals is further affected by factors not associated with rearing, such as the housing environment [Miller-Schroeder and Paterson, 1989; Nadler, 1982; Nadler and Collins, 1984], the lack of mate access [Wharton, 1995], partner incompatibility [Beck, 1982; Harcourt, 1978, 1987; Maple and Hoff, 1982], group instability, stress [Ogden et al., 1989, as cited in Loskutoff et al., 1991], medical problems [Gould, 1983; Reichard et al., 1990; Böer, 1983; Graham et al., 1991; Nadler and Collins, 1991; Loskutoff et al., 1991], and diet [Baer et al., 1989]. In some cases these may caused by not only one factor but by multiple factors. It is further necessary to consider that the situations under which types of rearing occur are variable also. The categories defined herein do not account for the quality of care, level of interaction with human caregivers, contact with peers, or methods of resocialization after non-mother-rearing.

CONCLUSIONS

1. In captivity, female ZB gorillas are as reproductively successful as WB gorillas.
2. Male WB gorillas are more reproductively successful than ZB males, probably due to the breeding status of the older males, with higher representation of WB individuals. There is a positive trend toward an increased reproductive success of CB males.
3. Female MR gorillas are more reproductively successful than both HR and PHR gorillas.
4. MR males are more reproductively successful, but the degree of reproductive success appears to not be affected by rearing type.
5. As mother-rearing positively impacts future reproductive success of gorilla offspring, the gorilla SSP® is justified in placing a strong emphasis on the management protocols that encourage maternal competence before and after the actual birth of an infant.

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