

DISTORTED SEX RATIO AT BIRTH IN THE CAPTIVE PYGMY HIPPOPOTAMUS, *HEXAPROTODON LIBERIENSIS*

SAMUEL ZSCHOKKE*

Department of Integrative Biology, Section of Conservation Biology (Institut für Natur-, Landschafts- und Umweltschutz), University of Basel, St. Johannis-Vorstadt 10, CH-4056 Basel, Switzerland

The total captive population of the pygmy hippopotamus *Hexaprotodon* (= *Choeropsis*) *liberiensis* has a highly female-biased sex ratio at birth (41% males), which exceeds most of the other known distorted sex ratios in captive mammals. Deviation from an even sex ratio was not compensated by a higher juvenile mortality in females. I examined the possible causes of that deviation and could not find any association between offspring sex and inbreeding, parity, or mother's age. I found, however, a significant difference in sex ratios among different zoological gardens, suggesting that husbandry influenced sex at birth in the pygmy hippopotamus. Further analysis suggested that high feeding intensity and "hands-on" husbandry favored production of daughters. However, not all the observed patterns and relationships could be explained by classic sex ratio theories.

Key words: captive breeding, feeding intensity, pygmy hippopotamus, selective abortion, sex ratio, ungulate

In mammals the observed sex ratio at birth is generally around 50% males, but empirical and theoretical studies have demonstrated and explained a number of deviations from the even sex ratio under a variety of circumstances (Clutton-Brock and Iason 1986; Hardy 1997; Hoefs and Nowlan 1994).

Classic sex ratio theory predicts that parents should invest equally in offspring of both sexes (Fisher 1930). When sons and daughters are equally costly, we can expect an even sex ratio. When offspring of 1 sex are more costly, we can expect a lower proportion of this sex. Furthermore, an increased juvenile mortality of 1 sex should favor initial production of this sex, leading to a sex ratio at birth that is biased toward that sex (Fisher 1930). During growth, the ratio would then be expected to reverse until, at weaning, the sex ratio becomes biased against the sex with higher juvenile mor-

tality. These predictions were empirically confirmed in mammals by Clutton-Brock and Albon (1982) and Clutton-Brock (cited as pers. comm. by Charnov 1982), who found a general pattern of male-biased sex ratios at birth with subsequent higher mortalities of males during early growth.

Trivers and Willard (1973) suggested that in those polygynous mammals, in which male reproductive success varies more than that of females and in which parental investment in a son can influence its future reproductive success, mothers in good condition should tend to produce more sons. Under these circumstances it can also be expected that a son is costlier than a daughter. In captive situations the condition of mothers has usually been linked to stress and feeding levels.

Williams (1979) extended the theory of Trivers and Willard (1973) to species with small, variable litter sizes. He suggested that mothers might trade off litter size

* Correspondent: samuel.zschokke@alumni.ethz.ch

against offspring sex. Mothers in good condition should produce 2 offspring of the less costly sex (daughters), whereas mothers in poorer condition should produce only 1 offspring but can then afford to produce a son.

In mammals, sex of offspring is determined by whether an X- or a Y-bearing sperm fertilizes the egg. Males produce X- and Y-bearing sperm in equal numbers as a consequence of meiotic cell division. A distorted sex ratio can, therefore, be achieved by both parents through selective restraining or killing of 1 type of sperm or by the mother through selective abortion of embryos of the unwanted sex (Krackow 1995). In either case offspring sex is determined around the time of conception.

Zoological gardens have begun to play an important role in preserving endangered species, and they must ensure successful reproduction of captive species. Additionally, zoos benefit economically from young animals by their attractiveness to visitors. Reproduction requires that zoos keep ≥ 1 pair of adult individuals (as artificial insemination is not established in most species, and the loan of adult males is often a complicated procedure). In species that are difficult to keep in groups, zoos often limit their stock to 1 breeding pair plus any current offspring. This makes it difficult for the species coordinator to find a place to house surplus animals of species with a distorted sex ratio (Faust and Thompson 2000). It is also difficult to interest additional zoos in keeping individuals of an endangered species if these zoos have to be content with keeping only individuals of the more common sex for an undetermined period (B. Steck, pers. comm.)

The pygmy hippopotamus (*Hexaprotodon liberiensis*) is similar to its larger cousin, the common hippopotamus (*Hippopotamus amphibius*), except that it is much smaller with a shoulder height of 70–80 cm and a weight of 250–270 kg (Dorst and Dandelot 1970; Estes 1991). The pygmy hippopotamus is mainly confined to tropical rain forests along rivers in Liberia, Sierra

Leone, and the Ivory Coast in West Africa; its occurrence in Nigeria and Guinea is disputed (Eltringham 1993). Because of its secretive lifestyle, very little is known about the biology of the species in the wild.

Pygmy hippopotami usually give birth to a single offspring after an average gestation of 199 days (Zschokke and Steck 2001). Twin births do occur but are very rare; of the 908 births recorded in the studbook, only 7 (0.8%) were twin births. Pygmy hippopotami have an estrous cycle of about 35 days. In captivity, both sexes reproduce at 3–32 years of age and live for 30–40 years (Wirz-Hlavacek et al. 2001).

Pygmy hippopotami are reported to live solitarily or in mother-offspring groups. They are mainly active in the late afternoon and early evening, feeding on a variety of herbs, ferns, and fruits (Bülow 1987; Hentschel 1990). In captivity, pygmy hippopotami are often kept alone because of their high level of aggression (Rahn 1978; G. Guldenschuh, pers. comm.). Aggressive behavior may partly be a consequence of their being kept in captivity. Observations of animals living in the Azagny National Park (Ivory Coast) suggest that they do not defend exclusive territories (Bülow 1987).

The pygmy hippopotamus has been classified as “vulnerable” by the International Union for the Conservation of Nature (Baillie and Groombridge 1996). The current number of wild pygmy hippopotami is not known but is estimated to be only a few thousand (Eltringham 1993; but cf. Hentschel 1990 who presented an estimate of 25,000 individuals in the Ivory Coast alone). In captivity, the species breeds well but suffers from high inbreeding rates that lead to increased juvenile mortality (Wirz-Hlavacek et al. 2001).

In the captive pygmy hippopotamus, only 41% of all newborns are male (Wirz-Hlavacek et al. 2001). In the present study, I examined factors that could be related to this uneven sex ratio. In particular, I compared the observed sex ratio at birth with factors that are known to be related to sex

ratio in other mammals, such as maternal stress, climatic effects, maternal nutrition, parity, and mother's age (Clutton-Brock and Iason 1986). In addition, I compared offspring sex with inbreeding because captive populations exhibit a high level of inbreeding and inbreeding is known to strongly affect juvenile survival in this species (Ballou and Ralls 1982; Ralls et al. 1979; Wirz-Hlavacek et al. 2001).

MATERIALS AND METHODS

Data on individual pygmy hippopotami were taken from the latest edition of the international studbook (Wirz-Hlavacek et al. 2001). In collaboration with the Basel Zoo (Basel, Switzerland), questionnaires concerning past and current husbandry practices were sent out in autumn of 1999 to all 18 zoos of the European Species Committee for the pygmy hippopotamus and to 13 selected zoos worldwide with an exceptional sex ratio at birth in the pygmy hippopotamus. Questionnaires were returned from all zoos of the Species Committee and from 9 of the other zoos (Appendix I). Additional data were obtained from an unpublished survey taken around 1992 by the former studbook keeper, K. Tobler (in litt.), and from Rahn (1978).

I analyzed the following husbandry-related factors, which could influence the sex ratio: zoo in which offspring was conceived, size of enclosure, water temperature, behavioral enrichment, single or multiple feeding per day, "hands-on" husbandry (direct handling of animal, with keeper and animal sharing the same unrestricted space) or "hands-off" husbandry (handling of animal with no contact made—Schmid 1998), and whether the animal was housed singly or in groups. In addition, I looked at the following individual traits: inbreeding (inbred or noninbred offspring), parity (primiparous or multiparous offspring), zoo generation (wild-born mother or captive-born mother), mother's age, identity of mother, identity of father, and interbirth interval.

Sex of embryos is determined at conception. If the mother aborts an embryo because it is of the unwanted sex, she is likely to do so as shortly after conception as possible to reduce costs. Consequently, I used the locality of conception of the offspring rather than the locality of birth in comparisons between zoos.

The questionnaires sent to zoos included a section on behavioral enrichment. Zoos were asked whether they offered behavioral enrichment in 3 categories: indoor foraging, outdoor foraging, and other (e.g., providing objects such as logs or branches that the animals could play with). I used the number of categories in which behavioral enrichment was offered to quantify the degree of behavioral enrichment offered.

Inbreeding coefficients were calculated from the studbook pedigree using the method described in Ballou (1983), and individuals were classified either as inbred (inbreeding coefficient $f > 0$) or as noninbred ($f = 0$).

Comparisons of sex ratio with continuous factors were made with unpaired *t*-tests. Comparisons with categorized factors were made with *G*-tests (Sokal and Rohlf 1995), except where the expected value in a cell was < 5 , in which case Fisher's exact test was used. Unless otherwise noted, offspring of unknown sex were omitted from the analyses.

RESULTS

The studbook listed the births of 915 pygmy hippopotami in captivity between 1919 and 2000 (Wirz-Hlavacek et al. 2001). Of these newborns, 360 were males, 519 were females, and 36 were of unknown sex. For offspring of known sex, this resulted in a sex ratio of 41.0% males, which differed from an even sex ratio (binomial test, *d.f.* = 1, $P < 0.0001$). Even if all offspring of unknown sex were considered to be males, the sex ratio would still be biased against males (43.3% males, *d.f.* = 1, $P < 0.0001$).

Juvenile survival (from birth up to 6 months) was lower in males (64.2%, $n = 358$) than in females (71.2%, $n = 514$; $G = 4.70$, *d.f.* = 1, $P = 0.030$). Disproportional survival resulted in an even more distorted sex ratio of 38.6% males ($n = 591$) at the age of 6 months, and at the age of 3 years, the approximate age at maturity, there remained only 37.5% males ($n = 480$).

It is not known whether the observed sex ratio is specific to captive births or whether it also applies to wild individuals. The only available indication of the sex ratio of the

TABLE 1.—Sex ratio of captive pygmy hippopotami born under various feeding regimes.

	Additional food							
	None		Grazing		Ad lib. roughage		Total	
	% male	<i>n</i>	% male	<i>n</i>	% male	<i>n</i>	% male	<i>n</i>
Single feeding	50.0	52	44.9	89	33.3	6	46.3	147
Multiple feedings	37.9	132	31.8	66	23.1	39	33.8	237

pygmy hippopotamus in its native habitat is the sex ratio of animals that were captured and brought into captivity. Of the 159 individuals imported from the wild, 70 were males, 84 were females, and 5 were of unknown sex. Considering only individuals of known sex, this corresponded to a sex ratio of 45.5% males. It is not known whether that observed ratio reflects the sex ratio in the wild or whether it was affected by sex-specific capture rates.

Sex ratio and husbandry.—Zoos with ≥ 20 conceptions differed in sex ratio at birth ($G = 18.35$, $d.f. = 8$, $P = 0.019$), which suggests that sex ratio was linked to husbandry or to genetic differences among zoo populations. A comparison of offspring sex ratio at birth among mothers and among fathers with ≥ 12 progeny revealed no individual differences (mothers, $G = 14.95$, $d.f. = 11$, $P = 0.185$; fathers, $G = 16.13$, $d.f. = 14$, $P = 0.306$), and I could not detect any indication that individuals with a biased sex ratio among their siblings produced offspring with the same bias in sex ratio. These findings suggest that differences in sex ratios among zoo populations were not genetic but were rather related to differences in husbandry between zoos.

Pygmy hippopotami that were fed more than once a day had a lower proportion of sons than those fed only once a day ($G = 5.95$, $d.f. = 1$, $P = 0.015$; Table 1). In addition, pygmy hippopotami that were allowed to graze or were given additional roughage ad libitum tended to produce fewer sons than those kept on a more restricted diet (Table 1).

There also seemed to be an association between sex ratio and whether animals

were handled or not—kept “hands-on” or “hands-off” (with no contact made—Schmid 1998). Fewer males were conceived by pygmy hippopotami that were kept hands-on (31.7% males, $n = 189$) than by those kept hands-off (48.2% males, $n = 168$; $G = 10.12$, $d.f. = 1$, $P = 0.002$). However, this association was linked closely to feeding frequency because all 9 zoos that worked hands-on fed several times per day, whereas only 7 of the 15 zoos that worked hands-off fed several times per day (Fisher’s exact test, $P = 0.010$).

Animals that were regularly (i.e., at least during the day) housed in pairs or in groups tended to produce more male offspring (43.6% males, $n = 291$) than those housed in separate enclosures except during mating (36.5% males, $n = 318$; $G = 3.25$, $d.f. = 1$, $P = 0.071$). However, the sex ratio did not seem to be affected by size of the enclosure ($t = 0.84$, $d.f. = 280$, $P = 0.401$), water temperature ($t = 1.41$, $d.f. = 291$, $P = 0.159$), or behavioral enrichment offered ($t = 0.66$, $d.f. = 368$, $P = 0.513$).

Sex ratio and individual traits.—I found no association between offspring sex and offspring inbreeding ($G = 0.34$, $d.f. = 1$, $P = 0.562$), parity (primiparous versus multiparous offspring; $G = 0.02$, $d.f. = 1$, $P = 0.880$), zoo generation (wild-born mother versus captive-born mother; $G = 0.24$, $d.f. = 1$, $P = 0.627$), or mother’s age ($t = 0.91$, $d.f. = 777$, $P = 0.364$). Likewise, there was no indication that sex ratio in twin births differed from sex ratio in single births; of the 6 twin births of known sex, 3 were male–female, 1 was female–female, and 2 were male–male ($G = 1.49$, $d.f. = 1$, $P = 0.223$).

The interbirth interval (log transformed) was found to be shorter after birth of a son (19.4 months, 95% confidence interval [CI]: 18.1–20.8) than after birth of a daughter (21.7 months, 95% CI: 20.3–23.3; $t = 2.21$, $d.f. = 692$, $P = 0.027$). Similarly, interbirth interval before birth of a son (19.3 months, 95% CI: 17.7–20.9) was shorter than before birth of a daughter (21.5 months, 95% CI: 20.2–22.8; $t = 2.08$, $d.f. = 690$, $P = 0.038$); twin births were excluded in these comparisons.

DISCUSSION

The total captive population of the pygmy hippopotamus had a highly female-biased sex ratio at birth. Of the 66 mammalian species whose sex ratio at birth in captivity was analyzed by Faust and Thompson (2000), only 2 showed a more female-biased sex ratio than did the pygmy hippopotamus, namely 33% of males in *Cephalophus monticola* (Artiodactyla: Bovidae) and 40% of males in *Cercocebus albigena* (Primates: Cercopithecidae). However, the small sample sizes used to calculate sex ratio in these 2 species (18 and 20 individuals, respectively) suggest that these figures are preliminary because sex ratios based on small sample sizes are more likely to be biased (Palmer 2000).

Classic sex ratio theory predicts that survival rates and parental investments should be higher for offspring of the rarer sex (Fisher 1930). In the pygmy hippopotamus, the opposite seems to be the case: offspring of the rarer sex, sons, had a lower juvenile survival rate, and there were some indications that sons are less costly than daughters. Although gestation periods and birth weights do not differ between sons and daughters (Lang 1975; Zschokke and Steck 2001), and costs of lactation could not be assessed because zoos differ greatly in the age at which pygmy hippopotami are weaned (Rahn 1978), the longer interbirth interval after the birth of a daughter and the higher survival rates of daughters indicate

higher investments per daughter than per son.

My results suggest that sex ratio at birth in the pygmy hippopotamus is linked to maternal feeding, with the proportion of sons decreasing under favorable feeding conditions. This parallels other studies that have shown a decrease in numbers of sons with increasing maternal nutrition or habitat quality in some deer, sheep, and goat species (Clutton-Brock and Iason 1986; Hoefs and Nowlan 1994). The reason for this relationship, however, is unclear; it is the opposite of the reaction predicted by the theory of Trivers and Willard (1973), which suggests that mothers in good condition should produce more offspring of the sex with the more variable reproductive success, i.e., sons.

For some species (e.g., mule deer—Kucera 1991), the decrease in proportion of sons with increasing maternal nutrition can be explained by the theory of Williams (1979), which suggests that mothers may trade off litter size against offspring sex, with mothers in better condition producing 2 offspring of the less costly sex (daughters), and mothers in poorer condition producing only 1 offspring of the more expensive sex (sons). However, this explanation is not applicable to the pygmy hippopotamus because it only very rarely gives birth to more than 1 offspring at a time, and the sex ratio in twins does not differ from that of singletons.

Most other studies that found the same association between maternal condition or nutrition and offspring sex ratio reported the proportion of sons to be much greater than 50% for poorly fed mothers (Clutton-Brock and Iason 1986), whereas in this study of the pygmy hippopotamus, even under the poorest feeding regime observed (single feeding, no additional food), the proportion of sons was only slightly greater than 50%. I suggest that this is because most zoos, to keep their animals in good condition, provide a high level of nutrition (Glatston 1997). In the present study, I

could therefore only compare normal feeding with high and very high feeding levels.

My results also suggest that sex ratio is linked to husbandry. Animals that were handled directly by the keeper, with the keeper being in their proximate vicinity (hands-on husbandry), had a lower proportion of sons than those that were handled without any contact (hands-off husbandry). Direct handling by the keeper may be stressful for this nonsocial animal. If direct handling is indeed associated with higher stress levels, and higher stress levels are linked to poor condition, then my results support the theory of Trivers and Willard (1973), which suggests that mothers in poor condition, i.e., with high stress levels, tend to produce fewer sons.

The mechanism of sex-ratio distortion in the pygmy hippopotamus is not known. However, the observed longer interbirth intervals before births of daughters (21.7 months, as opposed to 19.4 months for sons) is consistent with the mechanism of selective abortion, which causes a longer interbirth interval before the birth of the more common sex. Because pygmy hippopotami come into estrus roughly every month throughout the year, the costs of a delay in reproduction by an abortion shortly after fertilization are quite small.

The association observed between feeding frequency and hands-on versus hands-off husbandry is connected with the husbandry practice in hands-on husbandry of enticing animals with food morsels to follow the commands of the keepers. A reduction in feeding frequency—at 1st sight a possible recommendation for obtaining a more balanced sex ratio—is not possible without more extensive changes in husbandry. To obtain a more even sex ratio in the pygmy hippopotamus, I suggest that zoological gardens stop giving any food ad lib. and try to reduce the feeding frequency where possible. It may also be advantageous to keep the pygmy hippopotamus in pairs or groups rather than singly because group keeping may favor production of

sons. A more even sex ratio would facilitate breeding coordination among zoos, which in turn would allow a reduction of inbreeding, an essential prerequisite for the future survival of this species in captivity.

Most of the relationships observed are not in agreement with classic sex ratio theories of Fisher (1930) and Trivers and Willard (1973). It is especially striking that the rarer sex at birth (males) has a higher juvenile mortality and that females in apparently good condition (high feeding rates) produce more daughters. More research on the biology of the pygmy hippopotamus is needed before we can understand the patterns and relationships described in this study better.

ZUSAMMENFASSUNG

Die Zoopopulation des Zwergflusspferdes *Hexaprotodon* (= *Choeropsis*) *liberianensis* weist insgesamt einen starken Weibchenüberschüssen bei Geburt auf (59%). Dieser war grösser als die meisten bekannten Weibchenüberschüsse bei Geburt, und wurde nicht durch eine erhöhte Juvenil-mortalität der Weibchen ausgeglichen. In der vorliegenden Arbeit wurden verschiedene mögliche Ursachen dieses Weibchenüberschusses analysiert. Es konnte kein Zusammenhang zwischen dem Geschlechtsverhältnis einerseits und Inzucht, Parität und Alter der Mutter andererseits gefunden werden. Hingegen unterschieden sich die Geschlechtsverhältnisse zwischen den Zoos, was darauf hinweist, dass die Haltungsbedingungen das Geschlechtsverhältnis beim Zwergflusspferd beeinflussten. Eingehendere Untersuchungen ergaben, dass hohe Fütterungsraten und "hands-on" Haltung vermehrt zu weiblichem Nachwuchs führten. Nur wenige der beobachteten Zusammenhänge können durch die klassischen Theorien zum Geschlechtsverhältnis erklärt werden.

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APPENDIX I

The following zoos completed and returned our questionnaire: Ålborg Zoo, Ålborg, Denmark; Burgers' Zoo, Arnhem, The Netherlands; Basel Zoo, Basel, Switzerland; BREC's Baton Rouge Zoo, Baton Rouge, Louisiana; Tierpark Berlin-Friedrichsfelde, Berlin, Germany; Zoologischer Garten Berlin, Berlin, Germany; Taman Safari Indonesia, Bogor, Indonesia; Bristol

Zoo Gardens, Bristol, United Kingdom; Lincoln Park Zoo, Chicago, Illinois; Zoo Duisburg, Duisburg, Germany; Whipsnade Wild Animal Park, Dunstable, United Kingdom; Východočeská Zoologická Zahrada Safari Dvůr Králové nad Labem, Dvůr Králové nad Labem, Czech Republic; Edinburgh Zoo, Edinburgh, United Kingdom; Johannesburg Zoological Gardens, Johannesburg, South Africa; Kristiansand Dyrepark, Kristiansand, Norway; Zoo Leipzig, Leipzig, Germany; Memphis Zoo, Memphis,

Tennessee; Parc Zoologique de Paris, Paris, France; Ogród Zoologiczny Poznań, Poznań, Poland; Bioparco, Roma, Italy; Diergaard Blijdorp, Rotterdam, The Netherlands; Taronga Zoo, Sydney, Australia; Tallinna Loomaaed, Tallinn, Estonia; Zoologická Zahrada Ústí nad Labem, Ústí nad Labem, Czech Republic; Smithsonian National Zoological Park, Washington, D.C.; Marwell Zoological Park, Winchester, United Kingdom; and Zoo Zürich, Zürich, Switzerland.