

## RISK FACTORS ASSOCIATED WITH A SKEWED NATAL SEX RATIO IN CAPTIVE BLACK RHINOCEROSES (*DICEROS BICORNIS*) IN THE UNITED STATES

Patricia M. Dennis, D.V.M., Ph.D., Dipl. A.C.Z.M., Paivi J. Rajala-Schultz, D.V.M., Ph.D., Julie A. Funk, D.V.M., Ph.D., Evan S. Blumer, V.M.D., R. Eric Miller, D.V.M., Dipl. A.C.Z.M., Thomas E. Wittum, Ph.D., and William J. A. Saville, D.V.M., Ph.D., Dipl. A.C.V.I.M.

**Abstract:** The skew toward males in the sex ratio of calves is considered to be a problem for the captive population of black rhinoceroses (*Diceros bicornis*) in North America. This study used a retrospective case-control design to determine whether there was a predisposition toward birth of male calves over female calves and to examine risk factors associated with the occurrence of any detected skewed natal sex ratio in captive black rhinoceroses in the United States. The study population included captive female black rhinoceroses housed in the United States that had given birth to at least one calf of known sex. This study confirmed a skewing of the natal sex ratio toward male calves in the captive black rhinoceros population. The skewed ratio was found in calves born to wild-born dams, for which an increased time in captivity, irrespective of age, was associated with an increased likelihood of a male calf. Dams between 12 and 19 yr of age had a decreased likelihood of a male calf. The data also suggested a possible trend for the southern subspecies of black rhinoceros (*Diceros bicornis minor*) to be more likely to produce male calves than the eastern subspecies (*Diceros bicornis michaeli*). No associations were found with the sex of offspring in captive-born dams; however, this lack of association could be a result of low power in the study.

**Key words:** Black rhinoceros, *Diceros bicornis*, male calf, skewed sex ratio, wild-born dam.

### INTRODUCTION

The 2002 Rhinoceros Species Survival Plan (SSP) Masterplan (AZA SSP Rhinoceros Masterplan 2002. Prepared by the American Association of Zoos and Aquariums Rhino Advisory Group [AZA SSP Masterplan]) states that the skew toward males in the sex ratio of calves is a problem of major and increasing concern for the captive population of black rhinoceroses in North America. A study of the possible determinants of skewed natal sex ratios in captive black (*Diceros bicornis*) and Indian (*Rhinoceros unicornis*) rhinoceros in North America found that the eastern subspecies of black rhinoceros had a skewed offspring sex ratio that favored males (Atkinson, S. J. 1997. Possible determinants of skewed natal sex ratios in captive black (*Diceros bicornis*) and Indian (*Rhinoceros unicornis*) rhinoceros in North America. A report prepared for the International Rhino Foundation [IRF report]). A skewed sex ratio favoring males creates difficulties in managing these large, solitary animals in captivity. Unbalanced sex ratios can

compromise use of limited space in zoos. This study investigated whether there is a skewing of the sex ratio in captivity and examined risk factors that could be associated with a skewed ratio.

### MATERIALS AND METHODS

This study used a retrospective case-control design. Captive female black rhinoceroses housed in the United States that had given birth to at least one calf of known sex were included in the study. Information on the black rhinoceros was obtained from the 2001 International Studbook for the African Black Rhinoceros.<sup>11</sup> The outcome variable considered was the birth of a male calf.

Standard descriptive statistics summarized the data. Frequency distributions of categorical variables were evaluated, and means, medians, standard deviations, and ranges were calculated for continuous variables. Continuous variables were then categorized to facilitate analysis.

Age of dam at the birth of a calf was categorized into three groups. The categories were designed to reflect young, prime breeding age, and aging dams. Estimates vary on the age at which black rhinoceroses first reproduce<sup>6</sup> (Atkinson, S. J. 1997. IRF report), with an age at first conception reported to range between 3.8 and 12 yr. Gestation length is 14 to 16 mo.<sup>6</sup> On the basis of this information, we selected 0 to 12 yr for the young age group and approximately grouped animals into age tertiles. The categories were then adjusted to reflect the

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From the Department of Veterinary Preventive Medicine, The Ohio State University, 1920 Coffey Road, Columbus, Ohio 43210, USA (Dennis, Rajala-Schultz, Funk, Wittum, Saville); The Wilds, 14000 International Road, Cumberland, Ohio 43732, USA (Blumer); and the Saint Louis Zoo, One Government Drive, St. Louis, Missouri 63110, USA (Miller). Correspondence should be directed to William J. A. Saville (william.saville@cvm.osu.edu).

**Table 1.** Age and time in captivity at calving (yr) for wild-born and captive-born black rhinoceros dams.

	Wild-born dams		Captive-born dams	
	Female calf	Male calf	Female calf	Male calf
Age at calving				
<i>n</i>	55	78	30	34
$\bar{x}$	14.4	16.07	11.55	12.82
SD	6.54	7.16	4.66	5.18
Median	13.75	14.45	10.92	11.32
25th Percentile	9.37	10.9	8.52	9.36
75th Percentile	17.48	20.61	13.94	16.12
Range	5.15–35.64	5.08–36.92	5.74–27.66	4.82–24.18
Time in captivity at calving				
<i>n</i>	55	78		
$\bar{x}$	10.3	12.35		
SD	7.43	7.99		
Median	8.55	9.67		
25th Percentile	4.53	6.51		
75th Percentile	13.68	17.42		
Range	0.36–33.56	0.30–34.83		

overall younger ages of the captive-born dams. For wild-born dams, the age categories were age at birth of calf less than or equal to 12 yr, between 12 and 19 yr, and greater than 19 yr. For captive-born dams, the age categories were less than or equal to 10 yr, between 10 and 14 yr, and greater than 14 yr. The amount of time in captivity when the dam gave birth to the calf was also categorized into three groups for the wild-born dams—less than or equal to 7 yr; greater than 7 yr and less than or equal to 12 yr; and greater than 12 yr—approximately reflecting tertiles of the time in captivity. Offspring were categorized by subspecies as either southern black rhino or eastern black rhino. The dams were also categorized by housing: whether they had spent their entire time in captivity at one institution, two institutions, three institutions, or more than three institutions. Dams were also categorized on the basis of whether the calves were born before or after 1990. This time point was selected because of an observation that prevalence of several disease syndromes changed around this time (Dennis, unpubl. data).

All independent variables were screened for simple association with the outcome variable by calculating chi-square tests of homogeneity, odds ratios (ORs), and associated 95% confidence intervals (95% CIs). Variables were stratified by birth status of dam (whether wild-born or captive-born) in the model-building process to control for possible confounding. Variables that met a critical alpha level of 0.25 on the initial screening were included in the model construction. A generalized linear mixed

model was constructed with the use of a backward selection strategy. A generalized estimating equation was used to account for clustering at the level of the dam, given that many of the dams were multiparous. Development of the final multivariable model used a critical alpha level of 0.05 or a change in the parameter estimate greater than 20% as criteria to determine whether the variable acted as a confounder and should remain in the model.

## RESULTS

In the study population were 62 female black rhinoceroses, of which 34 were wild-born and 28 were born in captivity. The wild-born females produced 133 calves included in the study, of which 55 were female and 78 were male. The captive-born females produced 64 offspring included in the study, of which 30 were female and 34 were male. The mean age of the wild-born dams is  $23.56 \pm 9.24$  yr and for the captive-born dams is  $17.12 \pm 6.83$  yr. The age at calving for all dams was 4.82 to 36.92 yr, with a mean of 14.35 yr ( $\pm 6.51$  yr). The mean age at calving for wild-born females was  $15.38 \pm 6.93$  yr, with a range of 5.08 to 36.92 yr. The mean age at calving for the captive-born females was  $12.23 \pm 4.94$  yr, with a range of 4.82 to 27.66 yr. Table 1 demonstrates the mean age of dams at calving for female calves and male calves. At the time of the study, the dams had produced 1 to 13 offspring. The wild-born dams produced twice as many calves as the captive-born dams. The mean age at which captive-born dams gave birth was an average of 1.62 yr younger per parity than that of the corre-

**Table 2.** Age of black rhinoceros dam at calving by birth order of offspring.

Birth order	<i>n</i>	% of dams	$\bar{x}$	SD	Median	Percentile		Range
						25th	75th	
Wild-born								
1	34	100	8.85	2.96	8.18	6.83	10.08	5.08–17.80
2	28	82.35	12.62	3.61	12.12	9.73	14.18	6.79–20.02
3	23	67.65	15.8	4.32	15.89	12.82	17.51	8.89–26.46
4	18	52.94	17.79	4.52	17.2	14.47	19.71	10.76–27.97
5	11	32.35	20.36	5.19	20.24	17.22	25.69	12.71–28.59
6	5	14.71	22.23	5.84	22.82	19.56	24.03	14.44–30.29
7	4	11.76	24.94	6.98	24.21	19.75	30.13	17.46–33.88
8	4	11.76	26.97	7.78	26.64	20.51	33.44	18.97–35.64
9	2	5.88	28.73	11.58	28.73	20.54	36.92	20.54–36.92
10	1	2.94	24.58					
11	1	2.94	26					
12	1	2.94	27.5					
13	1	2.94	29.23					
Captive-born								
1	28	100	9.14	3.38	8.39	6.84	10.77	4.82–20.54
2	14	50.00	11.21	1.88	11.32	9.36	12.81	8.52–14.32
3	9	32.14	13.13	2.1	13.04	11.49	14.66	10.55–16.12
4	5	17.86	15.85	1.89	16.18	14.37	16.33	13.79–18.58
5	2	7.14	17.52	1.84	17.52	16.22	18.82	16.22–18.82
6	2	7.14	21.03	2.58	21.03	19.2	22.85	19.20–22.85
7	1	3.57	20.67					
8	1	3.57	22.67					
9	1	3.57	24.18					
10	1	3.57	27.66					

sponding parity for wild-born dams. Table 2 demonstrates the mean age per parity for the two groups, as well as the percentage in each parity group. A summary of the descriptive data is provided in Table 3.

Initially, variables were stratified by birth status of dam (whether wild-born or captive-born) in the model-building process to control for possible confounding. During initial model building, it became apparent that variables had widely different significance between the wild-born and captive-born groups. Therefore, separate models were built that considered whether offspring were born to wild-born dams or to captive-born dams. Independent variables were screened for simple association with the outcome variable of male calf. For the wild-born dams, the variables time in captivity and birth of offspring before or after 1990 met the critical alpha level of 0.25 and were included in the model. Neither dam's age at birth of calf nor subspecies met the critical alpha level; however, these two variables were forced into the model to control for them in data analysis. Of the variables evaluated for the captive-born dams, none were significant.

The final model is presented in Table 4 for wild-

born dams. For these dams, the variable subspecies did not meet the final critical alpha level of 0.05; however, removal of the variable caused a greater than 20% change in the estimates of the other variables, so the variable subspecies was left in the model to control for any confounding effect. Table 5 illustrates the final model for captive-born dams. Of the variables evaluated for the captive-born dams, none were significant.

Calves of wild-born dams were almost five times more likely to be male if the dam had been in captivity for greater than 12 yr (OR 4.85, 95% CI 1.25–18.74), and almost four times more likely to be male if the dam had been in captivity between 7 and 12 yr (OR 3.80, 95% CI 1.14–12.74) compared with the referent group of those dams in captivity less than or equal to 7 yr. Age of the dam at the time of the calf's birth was also significant, with dams between the ages of 12 and 19 yr having only a quarter the risk of having a male calf as those dams 12 yr or younger (OR 0.24, 95% CI 0.09–0.63). It is important to note the distinction between time in captivity and age of the dam. Although in many cases time in captivity might mirror age, this is not inherently true. Animals are brought into cap-

**Table 3.** Initial variables considered in model-building by gender of black rhinoceros calf.

	Wild-born dams			Captive-born dams		
	Female	Male	Total	Female	Male	Total
Age of dam at calving (yr)						
>19	10	25	35	2	5	7
>12 and <19	25	23	48	8	11	19
>0 and <12	20	30	50	20	18	38
Years in captivity at calving						
>12	18	31	49	10	16	26
>7 and <12	14	25	39	19	16	35
>0 and <7	23	22	45	1	2	3
Subspecies of dam						
<i>Diceros bicornis minor</i>	13	20	33	4	4	8
<i>Diceros bicornis michaeli</i>	42	58	100	26	30	56
Housing: number of institutions						
1 institution	28	40	68	6	12	18
>1 institution	27	38	65	24	22	46
Offspring born relative to 1990						
On or before 1990	38	46	84	16	16	32
After 1990	17	32	49	14	18	32
Generation						
Wild-born	55	78	133			
1st generation captive-born				23	23	46
2nd or 3rd generation captive-born				7	11	18

tivity at varying ages. Results of this study demonstrate an increased risk of producing a male calf with increasing time in captivity, but a decreased risk of a male calf if the dam is between the ages of 12 and 19 yr. The variable subspecies was not significant on the basis of a 0.05 critical alpha level but was borderline at  $P \leq 0.07$  (OR 2.42, 95% CI 0.93–6.32).

## DISCUSSION

Multiple hypotheses have been proposed attempting to explain the skewing of natal sex ratios. Some of the factors thought to influence the natal sex ratio include maternal condition, age, and timing of insemination.<sup>13,14,15</sup> One hypothesis suggests that the skewing of natal sex ratios is based on maternal condition.<sup>15</sup> The authors hypothesized that

**Table 4.** Final model for wild-born black rhinoceros dams.<sup>a</sup>

Variable	Estimate	SE	95% CI	P	OR	95% CI	
Age at calving (yr)							
>19	-0.5014	0.6321	-1.7402 to 0.7374	0.4277	0.61	0.18	— 2.09
12 < age < 19	-1.4189	0.4917	-2.3827 to -0.4552	0.0039	0.24	0.09	— 0.63
0 < age < 12	reference						
Time in captivity (yr)							
>12	1.5788	0.6897	0.227 to 2.9305	0.0221	4.85	1.25	— 18.74
7 < time < 12	1.3358	0.6169	0.1267 to 2.5448	0.0304	3.80	1.14	— 12.74
0 < time < 7	reference						
<i>Diceros bicornis minor</i>	0.8835	0.4898	-0.0765 to 1.8435	0.0713	2.42	0.93	— 6.32
<i>Diceros bicornis michaeli</i>	reference						

<sup>a</sup> CI, confidence interval; OR, odds ratio.

**Table 5.** Final model for captive-born dams. No significant variables were identified.

	Estimate	SE	95% CI	P
Age at birth of calf (yr)				
>14	0.9351	0.7293	-0.4944 to 2.3646	0.1998
10 < age < 14	0.2603	0.6812	-1.0748 to 1.5954	0.7024
0 < age < 10	reference			
First generation captive-born	-0.4419	0.5978	-1.6135 to 0.7298	0.4598
Second or third generation	reference			
<i>Diceros bicornis minor</i>	-0.0265	0.9554	-1.8991 to 1.8461	0.9779
<i>Diceros bicornis michaeli</i>	reference			
Housed at one institution	0.637	0.6793	-0.6943 to 1.9684	0.3483
Housed at 2 different institutions	-0.2318	0.8256	-1.85 to 1.3865	0.7789
Housed at 3 institutions	0.0034	0.5932	-1.1593 to 1.1661	0.9954
Housed at >3 institutions	reference			
Offspring born before or during 1990	-0.1925	0.5583	-1.2868 to 0.9018	0.7302
Offspring born after 1990	reference			

<sup>a</sup> CI, confidence interval.

natural selection favors parental ability to adjust the sex ratio of offspring produced on the basis of parental ability to invest in the offspring.<sup>15</sup> As adult females vary from the average body condition of females, there is a tendency to bias the production of their young toward one sex or the other, whichever will have the greatest reproductive success. This hypothesis assumes some tendency for the condition of the offspring at the end of parental investment to be maintained into adulthood. For polygynous species, the tendency is for females in good condition to produce male offspring, whereas females in poor condition tend to produce female offspring. In polygynous species, better adult condition affects the reproductive success of the male more than the female. The male in better condition can exclude other males from breeding and sire many offspring himself, whereas a male in poor condition is not likely to sire any offspring because he will be driven away from the females by the better conditioned males. The female in good condition only shows a moderate increase in reproductive success by producing one offspring. This hypothesis has been supported by studies in several species, including several species of deer (*Dama dama*, *Cervus elaphus*),<sup>4,5</sup> sheep (*Ovis musimon*),<sup>8</sup> mice (*Mus musculus*),<sup>9</sup> and several bird species (*Tachycineta bicolor*).<sup>10,17</sup> The biological mechanism for skewing of natal sex ratios is unknown.

A permutation of the maternal condition hypothesis is one that suggests maternal age influences the sex ratio. In sexually dimorphic large mammals, faster growth rates in males make them more susceptible to food shortages, both in utero and postnatally.<sup>1</sup> There is evidence in multiple species that

male offspring are heavier at birth, born later, and suckle more frequently and until a later age than female offspring (Atkinson, S. J. 1997. IRF report). Because of the high energy demands of male offspring, only mothers in good condition would be expected to have sufficient resources to produce surviving sons. The females of many large mammal species become reproductively active before achieving their adult body weight.<sup>1</sup> As they reach the end of their reproductive life, their body condition diminishes. Thus, based on the maternal condition hypothesis, the sex ratio of male calves to female calves would be expected to be low in young and aging breeding females and high in females of prime breeding age.<sup>3</sup> It has been pointed out, however, that in some species, young or nulliparous dams are in superior body condition compared with middle-aged or multiparous females; thus, the younger dams would be more likely to produce male offspring.<sup>2</sup>

Another suggested hypothesis to explain skewing of sex ratios is based on the timing of fertilization. This hypothesis proposes that males are produced when insemination occurs close to the time of ovulation, and females are produced when insemination occurs before or remote from the time of ovulation.<sup>14</sup> The rationale behind this proposal is that Y-bearing spermatozoa are more motile or better able to penetrate the membrane of the unfertilized egg, but do not survive as long as X-bearing spermatozoa.<sup>14</sup> Evidence supporting this hypothesis is found in several species of mammals, including white-tailed deer (*Odocoileus virginianus*),<sup>16</sup> Barbary macaques (*Macaca sylvanus*),<sup>12</sup> hamsters (*Mesocricetus auratus*),<sup>13</sup> and rats (*Rattus norvegicus*).<sup>7</sup>

Although the data are not available in this study to examine the third hypothesis in relation to the skewed sex ratio in captive black rhinos, the first two hypotheses warrant further consideration in light of our findings. The finding that there is an increased likelihood of producing a male calf with greater time in captivity for the dam could support the hypothesis that increased body condition of the dam increases the likelihood of producing a male calf. The regular availability of food and its more consistent quality, without the need to travel great distances to obtain it, could result in increased body condition of captive animals compared with those in the wild. There is a clear association between increased time in captivity and production of male calves by wild-born dams. Although previous research suggests that the particular characteristic of captivity that influences the production of male calves is improved body condition of the dam, this cannot be determined by this study. Determination of this particular characteristic requires further research.

The influence of age on likelihood of having a male calf supports the hypothesis<sup>15</sup> that dams are more likely to produce one sex of offspring during prime breeding years, and the opposite sex during the early and late breeding years. The difference, however, is that these data suggest that the tendency is to produce female calves during the prime breeding years and male calves in the early and late breeding years.

Inclusion of the predictor variables of age at birth of calf and time in captivity at birth of calf presents a challenge because of the possibility that these variables are highly correlated. That is, the older a captive animal, the longer it has been in captivity. These two variables, however, do not completely map each other because the wild-born dams were brought into captivity at varying ages; thus, greater age does not necessarily equate to a greater time in captivity.

An interesting finding of this study was the presence of a skewed natal sex ratio only in the offspring of wild-born dams and not captive-born dams. This difference could reflect the older age of the wild-born dam population. The wild-born dam population includes more animals that have entered into the older age group that produces more male calves, whereas more of the captive-born dams are still in the 12 to 19 yr bracket that tends to produce more female calves. It could be that as the captive-born dam population ages, a skewing of the natal sex ratio favoring males occurs. Another explanation for the absence of a skewed sex ratio in the calves of captive-born dams is the decreased statis-

tical power because of the fewer number of calves born to captive-born dams.

It is also interesting to note that the wild-born dams produced twice as many calves as the captive-born dams. Although the captive-born dams are younger than the wild-born dams, younger age alone cannot explain the discrepancy in number of offspring between the two groups, especially considering that the mean age for both groups at the time of the first calf is approximately 9 yr of age. It remains unknown why captive-born dams are not producing as many calves as their wild-born counterparts. Breeding management of the two groups could not be examined as part of this study because historic husbandry information was not available. It is possible that population management decisions are the controlling factors governing the discrepancy between wild-born and captive-born calf production. It could be that the wild-born dams, representing the founder population, were bred more often than captive-born dams, thus creating a significantly larger number of calves born to wild-born dams. Although this factor was not considered in this study, further investigation to determine whether management decisions are influencing calf production is warranted.

The AZA SSP Masterplan (2002) lists the development of methods for in utero sex determination of fetuses as a research priority for reproductive research on all rhinoceros species. Presumably the development of these methods would enable the early termination of pregnancies with unwanted male calves. However, with increased time in captivity as a risk factor for male calf production in wild-born dams, this strategy might not prove that effective at correcting the skewed natal sex ratio in the captive black rhinoceros population. Directing efforts to identify the characteristic of captivity that is associated with this increased risk, identifying factors affecting decreased calf production by captive-born dams, and focusing breeding efforts on the dams in the age group of 12 to 19 yr could better serve to correct the skewed sex ratio.

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#### LITERATURE CITED

1. Clutton-Brock, T. H., S. D. Albon, and F. E. Guinness. 1985. Paternal investment and sex differences in ju-

- venile mortality in birds and mammals. *Nature* 313: 131–133.
2. Clutton-Brock, T. H., F. E. Guinness, and S. D. Albon. 1982. *In: Red Deer: Behavior and Ecology of Two Sexes*. Univ. of Chicago Press, Chicago, Illinois. 378 p.
  3. Clutton-Brock, T. H., and G. R. Iason. 1986. Sex ratio variation in mammals. *Q. Rev. Biol.* 61: 339–374.
  4. Enright, W. J., L. J. Spicer, M. Kelly, N. Culleton, and D. J. Rendiville. 2001. Energy level in winter diets of fallow deer: effect on plasma levels of insulin-like growth factor-I and sex ratio of their offspring. *Small Ruminant Res.* 39: 253–259.
  5. Flint, A. P. F., S. D. Albon, and S. I. Jafar. 1997. Blastocyst development and conceptus sex selection in red deer *Cervus elaphus*: Studies of a free-living population on the Island of Rum. *Gen. Comp. Endocrinol.* 106: 374–383.
  6. Hall-Martin, A. J. 1986. Recruitment in a small black rhino population. *Pachyderm* 7: 6–8.
  7. Hedricks, C., and M. K. McClintock. 1990. Timing of insemination is correlated with the secondary sex ratio of Norway rats. *Physiol. Behav.* 48: 625–632.
  8. Landete-Castillejos, T., A. Garcia, S. Langton, I. Inglis, L. Gallego, and J. Garde. 2001. Opposing offspring sex ratio variations with increasing age and weight in mouflon mothers (*Ovis musimon*). *Acta Vet. Hung.* 49: 257–268.
  9. Meikle, D., and M. Westberg. 2001. Maternal nutrition and reproduction of daughters in wild house mice (*Mus musculus*). *Reproduction* 122: 437–442.
  10. Nager, R. G., P. Monaghan, R. Griffiths, D. C. Houston, and R. Dawson. 1999. Experimental demonstration that offspring sex ratio varies with maternal condition. *Proc. Natl. Acad. Sci. USA* 96: 570–573.
  11. Ochs, A. 2001. *International Studbook for the African Black Rhinoceros*. Zoologischer Garten, Berlin, Germany.
  12. Paul, A., and J. Kuester. 1987. Sex ratio adjustments in a seasonally breeding primate species: evidence from the Barbary macaque population of Affenberg, Salem. *Ethology* 74: 117–132.
  13. Pratt, N. C., U. W. Huch, and R. D. Lisk. 1987. Offspring sex ratio in hamsters is correlated with vaginal pH at certain times of mating. *Behav. Neural Biol.* 48: 310–316.
  14. Reubinoff, B. E., and J. G. Schenker. 1996. New advances in sex preselection. *Fertil. Steril.* 66: 343–350.
  15. Trivers, R. L., and D. E. Willard. 1973. Natural selection of parental ability to vary the sex ratio of offspring. *Science* 179: 90–91.
  16. Verme, L. J., and J. J. Ozoga. 1981. Sex ratio of white-tailed deer and the estrous cycle. *J. Wildl. Manage.* 45: 710–715.
  17. Whittingham, L. A., and P. O. Dunn. 2000. Offspring sex ratios in tree swallows: females in better condition produce more sons. *Mol. Ecol.* 9: 1123–1129.

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