

Birth sex in an expanding black rhinoceros (*Diceros bicornis minor*) population

PETER R. LAW,* BRAD FIKE, AND PETER C. LENT

4 Mack Place, Monroe, NY 10950, USA (PRL)

P.O. Box 433, Grahamstown, 6140, Republic of South Africa (BF)

Department of Zoology and Entomology, University of Fort Hare, Alice, 5700, Republic of South Africa (PCL)

* Correspondent: prldb@member.ams.org

Despite a now-extensive literature on sex allocation, facultative sex allocation in mammals remains controversial. We studied the complete birth-sex record of a black rhinoceros (*Diceros bicornis minor*) population from its reintroduction in 1986 through 2008. Neither explicit models of birth sex as Bernoulli trials nor mixed-model logistic regression yielded evidence for an influence on birth sex of birth sequence, maternal identity, year of conception, rainfall, population size, maternal age, or adult sex ratio despite a small female-biased population birth sex ratio that nevertheless appears to be unusual for black rhinoceros. One interpretation of our results is that our study population did not facultatively control birth sex, either because black rhinoceros cannot or because environmental and demographic circumstances did not elicit conditions that favor pronounced adaptive control of birth sex in this population. Alternatively, variation in sex allocation could have occurred in a manner not captured by our modeling or at a scale we could not probe. If the observed female bias is not purely stochastic, it may result from the perturbed age structure of the introductions, which was biased toward subadults.

Key words: birth sex, black rhino, *Diceros bicornis*, local resource competition, maternal state, sex allocation

© 2014 American Society of Mammalogists

DOI: 10.1644/13-MAMM-A-175

Evolutionary explanations of sex allocation began with Darwin and are now represented by an extensive literature (Charnov 1982; Frank 1998; Hardy 2002; West 2009), reflecting the intrinsic interest of sex allocation and its importance for demography and conservation. Sex allocation in mammals remains enigmatic, however, both as regards potential mechanisms of facultative sex determination (Krackow 2002; Pen and Weissing 2002; but see Cameron 2004; Roche et al. 2006; Cameron and Linklater 2007; Cameron et al. 2008; Helle et al. 2008) and theoretical expectations (Cockburn et al. 2002).

Early adaptive hypotheses tended to explain or predict deviations from equal investment in the sexes or 1:1 sex ratios by focusing on particular aspects of life-history strategy, for example, the Trivers–Willard and local resource competition hypotheses (Cockburn et al. 2002; West 2009). An integrated approach to modeling sex allocation that incorporates factors and strategies contributing to the reproductive value of offspring, mechanisms of sex determination, and nonadaptive influences (Leimar 1996; Pen and Weissing 2002; Sheldon and West 2004; Isaac et al. 2005; Schwanz et al. 2006; Wild and West 2007) is preferable. Observations of biased birth sex ratio

(BSR) for a population demand explanation, but the absence of bias in a population-level record does not preclude variation among individuals or across space or time because such variation may average out at the population level (Frank 1987; West 2009). On the other hand, evidence for the absence of variation in sex allocation also is of interest and moreover combats publication bias (Festa-Bianchet 1996).

Although experimental studies are required to resolve outstanding issues, investigation of sex allocation in natural populations is of fundamental interest. Among mammals, large ungulates have attracted considerable attention in sex allocation studies (West 2009). Owen-Smith (1988) suggested that megaherbivores in particular possessed scope for facultative adjustment of sex allocation due to flexible birth intervals and aseasonal reproduction. Furthermore, several studies reported evidence for variation in sex allocation in black rhinoceros (*Diceros bicornis*—Hrabar and du Toit 2005; Berkeley and Linklater 2010; Weladji and Laflamme-Mayer 2011).



We studied the birth-sex record of an expanding population of black rhinoceros (*Diceros bicornis minor*) over 22 years from its reintroduction, with the aim of detecting influences on birth sex. Intensive and consistent monitoring of the population throughout the study period yielded reliable records of births and deaths that minimized concerns that results might be affected by unknown births (Fike 2011).

Which hypothetical influences on sex allocation are particularly relevant to black rhinoceros? Because black rhinoceros are polygynous and males presumably exhibit a greater variance in reproductive success than females (Garnier et al. 2001), the Trivers–Willard hypothesis suggests that females in good condition at conception should favor male offspring but otherwise produce female offspring, assuming that greater maternal investment translates into increased reproductive value of offspring. However, Owen-Smith (1988) argued that successful male and female black rhinoceros would exhibit little differential lifetime reproductive success. Among ungulates, browsers such as black rhinoceros may be better candidates for the local resource competition hypothesis than grazers (Kojola 1998). If males disperse, then the local resource competition hypothesis predicts a male bias in response to resource competition, either due to adverse conditions or increasing density (as in Visscher et al. 2004; Weladji and Laflamme-Mayer 2011). On the other hand, adverse conditions or increasing density also might act as adaptive or nonadaptive influences on the secondary sex ratio through induced stress (Kruuk et al. 1999; Mysterud et al. 2000; Linklater 2007), possibly creating a female bias if male offspring involve greater maternal investment.

Maternal age may influence sex allocation in several ways. Because maternal reproductive value varies with age, the trade-off between investment in survival and reproduction varies (Charlesworth 1994), with possible consequences for sex allocation if maternal costs and offspring reproductive value depend on offspring sex (Charnov 1982; Hogg et al. 1992; Martin and Festa-Bianchet 2011). Increasing maternal experience with age may result in greater reproductive success (Cameron et al. 2000) and thereby affect the predictions of the Trivers–Willard hypothesis (Côté and Festa-Bianchet 2001). Maternal age also has been proposed as a major component of maternal condition in the Trivers–Willard hypothesis (Saltz 2001; but see Hewison et al. 2002; Saltz and Kotler 2003), with prediction of a bias in male offspring for mothers of prime age. Maternal age also may interact with the local resource competition hypothesis (Isaac et al. 2005) by favoring the dispersing offspring sex at different maternal ages, for example, at an early maternal age to avoid future resource competition with offspring. Finally, a homeostatic hypothesis (Cockburn et al. 2002) suggests that sex allocation may respond to the adult sex ratio.

Clearly, a priori prediction of birth sex for a population based on these complex and competing hypotheses is impractical. To detect influences on birth sex, we modeled birth sex via logistic regression using covariates of ambient conditions and components of maternal state at conception

chosen based on the above considerations (see “Materials and Methods” for details), and interpreted our results in the light of the sex allocation literature. This analysis was limited by the available covariates; for example, we lacked a measure of maternal condition required to directly address the Trivers–Willard hypothesis.

Hrabar and du Toit (2005) reported that offspring sex tended to alternate in the calf sequences of female black rhinoceros of their study but found no evidence for a sex bias in 1st calves, possibly indicating relationships between offspring sex and maternal investment and experience, respectively. We assessed the relevance of birth order and sex of the previous birth by modeling birth-sex sequences as Bernoulli trials.

Evidence for facultative sex allocation in black rhinoceros would be highly relevant to their demography and management, especially reintroduction. A reintroduced population begins with a perturbed age distribution, and during the initial expanding phase females may experience reduced intrasexual competition for resources more than males experience reduced competition for reproductive opportunities. Because females also have reproductive value more evenly distributed over age than males, a bias in female offspring sex might be favored after reintroduction (West and Godfray 1997) independently of other considerations. We explored this possibility by examining cumulative BSRs modeled as Bernoulli trials.

MATERIALS AND METHODS

Study area.—The Great Fish River Reserve, Eastern Cape Province, South Africa, is split into halves by the Great Fish and Kat rivers. In each half, black rhinoceros populations were independently introduced, managed, and monitored. The population in the western Sam-Knott-Kudu-Reserve (SKKR) sector (220 km²) is the older, larger, and more consistently monitored of the 2; we refer to it from its founding in 1986 through 2008 as the SKKR population. The SKKR population was effectively demographically isolated and little affected by the managed removal of 5 subadults in 2006. The Great Fish River Reserve is considered excellent black rhinoceros habitat (Ganqa et al. 2005). In particular, SKKR black rhinoceros as of 2004 appeared to meet their nutritional and energetic needs without selective feeding (van Lieverloo et al. 2009). The SKKR population was monitored under BF’s direction as reserve manager by ground patrols and aerial reconnaissance; each animal was ear notched, and births and deaths were routinely recorded as part of routine monitoring. No animals were handled for the research reported in this paper.

Study population.—The SKKR population was founded through the introduction of 13 males and 15 females (of which only 3 each were already adults) in 5 independent introduction events between June 1986 and December 1997. Each introduction comprised as near to an equal sex ratio as possible, but 3 males and 2 females died too soon after release to contribute to the population. In 2003, 1 female immigrated into the western sector from the eastern sector just prior to her 1st calving (the only exception to demographic isolation during

TABLE 1.—Cumulative birth sex ratio. $M:F$ is the number of males (M) and number of females (F) of *Diceros bicornis minor* born from reintroduction of the population through the specified year; ratio is $M/(M + F)$; 1-sided p is the probability of observing F or more females in an unbiased Bernoulli trial of length $M + F$. Pop Size is the population size and ASR is the adult sex ratio (the number of adult males : females), both at the end of the calendar year.

Year	$M:F$	Ratio	1-sided p	Pop Size	ASR
1988	0:1	0	0.5	4	1:1
1989	0:1	0	0.5	7	1:1
1990	0:2	0	0.25	10	1:3
1991	1:3	0.25	0.313	11	1:4
1992	2:4	0.333	0.344	14	1:4
1993	2:5	0.286	0.227	15	3:4
1994	3:8	0.273	0.113	19	3:5
1995	5:8	0.385	0.291	21	3:6
1996	6:8	0.429	0.395	22	3:8
1997	6:12	0.333	0.119	39	4:8
1998	9:13	0.409	0.262	42	4:8
1999	9:17	0.346	0.084	46	5:9
2000	9:18	0.333	0.061	46	6:12
2001	16:22	0.421	0.209	57	6:17
2002	16:25	0.390	0.106	59	10:18
2003	20:32	0.385	0.063	70	14:20
2004	23:37	0.383	0.046	77	15:23
2005	29:41	0.414	0.094	84	15:24
2006	36:48	0.429	0.115	93	17:27
2007	41:50	0.451	0.201	98	16:27
2008	46:58	0.442	0.140	110	16:29

the study period) and is treated as a founding member of the SKKR population. The population grew monotonically on an annual basis to reach 110 at the end of 2008, consisting then of 26 calves, 39 subadults, and 45 adults (see also Table 1). Defining 3 maternal age classes by < 10 years (young), 10–24 years (prime age), and ≥ 25 years (old), the distribution of maternal ages was (3, 3, 1), (7, 7, 1), and (3, 22, 1) at the end of 1996, 2002, and 2008, respectively. Further information about the population and locale may be found in Lent and Fike (2003), Fike (2011), and Law et al. (2013).

Sex ratios are described either as the (nonreduced) ratio of the number of males (M) to the number of females (F), $M:F$, or as the proportion of males: $M/(M + F)$. The population sex ratio at the end of 2008 was 48:62 (43.6% male), and this apparent female bias may be attributed almost exclusively to the birth-sex record of 104 births with sex ratio 46:58 (44.2% male [Supporting Information S1, DOI: 10.1644/13-MAMM-A-175.S1]).

Upon detection, BF assigned each new individual a birth date and an interval of uncertainty in months centered on the nominal birth date (d), specified by a value U so that the interval of uncertainty is $d - U$ to $d + U$. The intervals of uncertainty of birth dates determined the accuracy with which some covariates of birth sex were assigned values. Conception was dated as 15 months prior to birth (Owen-Smith 1988).

Statistical analyses.—For each analysis, individual birth sex was the unit of interest and the set of SKKR birth sexes analyzed was the population of study, not a sample from which inference was made to some larger population. Our analyses

involved model construction, parameter estimation by maximum likelihood, and model comparison using the Akaike information criterion (AIC), specifically the 2nd-order corrected AIC (AIC_c), because sample size (n) was small relative to the number (K) of estimated model parameters ($n/K < 40$ —Burnham and Anderson 2002).

Because any sequence of binary events can be modeled as a Bernoulli trial (Williams et al. 2002) and chromosomal sex determination suggests modeling birth sex as an unbiased Bernoulli trial, we first compared models of the population BSR as unbiased and biased Bernoulli trials (Bernoulli analysis I [see Supporting Information S1]). We then investigated possible influences on birth sex employing logistic regression models of the probability of male birth sex, concentrating on the a priori choice of potential predictors but without presuming in which combinations such predictors might act. We used AIC_c to rank all 2^k models constructible from a choice of k fixed effects (random effects were employed in all models). The sum of Akaike weights, over the models in which a given predictor occurs, provides a measure of variable importance called “relative importance” (Burnham and Anderson 2002). Employing all 2^k models also guarantees balanced representation of the predictors for computation of relative importance (Doherty et al. 2012). We used the top-ranked models and the relative importance of the chosen variables to assess whether the latter provided an explanation of birth sex in the study population (Converse et al. 2006; Trimble et al. 2009). Following the guideline of using no more than $K = n/10$ structural parameters in univariate modeling (Burnham and Anderson 2002:245), we chose for the logistic regression those effects available to us that have received the most attention in the literature.

Several studies of sex allocation included a year effect as a random factor (Mysterud et al. 2000; Côté and Festa-Bianchet 2001; Proffitt et al. 2008; Martin and Festa-Bianchet 2011). For each model, we included random effects for maternal identity and year of conception, even though the number of births per mother and conceptions per year varied, including some singleton counts (Gelman and Hill 2007). We therefore limited fixed effects to 5 predictors, resulting in 8 structural parameters for the most complicated model (our “global” model) and 32 models in total, including the “base” model with no fixed effects, but just an intercept and the 2 random effects.

Of the interacting potential influences discussed in the Introduction, we included as fixed effects maternal age, population size, and adult sex ratio (i.e., the proportion of adult males among all adults), each measured at conception. For adult sex ratio, we defined a female black rhino as adult at 1st calving or at the 7th birthday, whichever came first, and a male black rhino as adult at his 8th birthday (Emslie et al. 1995; Law et al. 2013). We also included the cumulative rainfall during gestation (GestRain) as a measure of the influence of adverse conditions on the secondary sex ratio (Kruuk et al. 1999; Garroway and Broders 2007; Weladji and Laflamme-Mayer 2011). Because of the relationship between rainfall and primary production in African savannas (Shorrocks

2007), rainfall has been investigated as a possible influence on sex allocation via its influence on maternal condition (Visscher et al. 2004; Hrabar and du Toit 2005; van Hooft et al. 2010; Berkeley and Linklater 2010; Weladji and Laflamme-Mayer 2011). Lacking a measure of maternal condition appropriate for addressing the Trivers–Willard hypothesis directly, we resorted to rainfall, employing the cumulative rainfall over the 7 months ending with the month of conception (PriorRain7), as indicating a component of maternal state (Martin and Festa-Bianchet 2011). See Supporting Information S1 for details of precipitation.

Using nominal conception dates to assign seasonal year either made no difference to the assignment or was more likely to slightly reduce, rather than increase, the sex ratio in a few specific years. The assignment of maternal age, population size, and adult sex ratio was little affected by intervals of uncertainty with $U < 12$, but values of the 2 rainfall measures could be affected. We therefore considered 2 data sets for the logistic regression modeling: BS89, the 89 births for which intervals of uncertainty had $U \leq 3$, together with the predictors specified above; and BS103, the 103 births for which intervals of uncertainty had $U \leq 6$. For BS103, in place of PriorRain7 and GestRain, we used PriorRain12 and PriorRain24, the cumulative rainfall over the 12-month period ending with the month of conception and the cumulative rainfall over the 12-month period prior to that, respectively. PriorRain12 is less sensitive to the intervals of uncertainty with $U > 3$ than is PriorRain7 and has been used previously (Visscher et al. 2004; Weladji and Laflamme-Mayer 2011). PriorRain24 tested for a delayed effect of rainfall on primary production (van Hooft et al. 2010). Each data set had 28 maternal identities, BS89 had 19 random years, and BS103 had 20. The observed sex ratio was 0.449 for BS89 and 0.447 for BS103. We computed descriptive statistics for the fixed effects (Supporting Information S1) and then mean centered the covariates for analyses.

Analyses were conducted using R 2.10.1 (R Development Core Team 2009). For the fixed effects of each data set, we first computed pairwise correlations and variance-inflation factors, using function `corvif` from package `AED` (Zuur et al. 2009). Logistic regressions were constructed as generalized linear mixed models using function `lmer` in R package `lme4`. We followed the recommendation of Hosmer and Lemeshow (2000) to employ a combination of tests to assess both calibration (fit to data) and discrimination of our global model (Supporting Information S1). We also investigated both interactions between fixed effects and a nonlinear form for maternal age (Saltz 2001) by using generalized additive mixed models using the R package `gamm4`, for consistency with `lme4`.

To investigate the possible dependence of birth sex on birth order and sex of the previous birth, we modeled birth sequences as Bernoulli trials. Because of sparseness of data, we only modeled 1st through 5th births and called this analysis Bernoulli analysis II, in which models M_0 and M_1 were of the same form as in Bernoulli analysis I. M_2 modeled 1st births and subsequent births as independent Bernoulli trials. M_3 modeled

1st births as an independent Bernoulli trial and for subsequent births modeled the probability of male birth as dependent upon the sex of the prior birth. M_4 modeled each birth order as an independent Bernoulli trial. In their study, Hrabar and du Toit (2005) counted 17 calves preceded by a calf of opposite sex versus 9 preceded by a calf of the same sex. In our study, 31 calves were preceded by a calf of opposite sex, whereas 45 were preceded by a calf of same sex; specifically, 14 MF (i.e., male then female) births, 17 FM births, 18 MM births, and 27 FF births, which exhibited a greater skew in FF births than the corresponding counts modeled by M_3 in Bernoulli analysis II (12 MF, 14 FM, 16 MM, and 20 FF). Together with the 26 firstborn calves, these data total 102 births (excluding only the calves born first in SKKR to the 2 females imported as adults, because their birth order is unknown). As a further check on the relevance of previous birth sex, therefore, for Bernoulli analysis III we modeled these 102 birth sexes using models M_0 , M_1 , and M_3 of Bernoulli analysis II.

Finally, to assess whether the perturbed age structure due to reintroduction influenced sex allocation, we computed the cumulative BSR over time and repeated Bernoulli analysis I for the most unlikely female bias as judged by a 1-sided binomial test for an unbiased Bernoulli trial (Bernoulli analysis IV), interpreting the result with caution.

RESULTS

For the population BSR, the evidence ratio for the model M_0 as an unbiased Bernoulli trial versus the model M_1 as a biased Bernoulli trial was only 1.38 (Bernoulli analysis I [Table 2]). The model-averaged probability of male birth in this analysis was $\theta = 0.476$, with unconditional *SE* of 0.057.

For each data set BS89 and BS103 all pairwise correlations between fixed-effect predictors had magnitude < 0.3 and all variance-inflation factors were < 2 , indicating no correlations of concern between predictors. PriorRain24 received the least support of the 5 fixed effects in BS103; otherwise the modeling of the 2 data sets performed similarly, with PriorRain12 behaving analogously to PriorRain7 in BS89. Hence, we only report on the BS89 data, but see Supporting Information S1.

The tests of calibration of the global logistic regression model indicated the fitted values of the global generalized linear model were consistent with the data, whereas the fitted values returned by `lmer` for the global generalized linear mixed model were marginally consistent with the data. The global generalized linear mixed model had better discrimination than the global generalized linear model and was rated “acceptable” (Supporting Information S1).

All 32 models fell within 10 units of the top-ranked model, which was the base model, and ΔAIC_c increased approximately with the number of parameters in the model, with the global model ranked last (Table 3). No model was clearly singled out by ΔAIC_c , nor did the relative importance strongly single out any fixed effects, suggesting only a slight preference for PriorRain7 and perhaps population size, but regression coefficients for the global model indicated weak effects, if

TABLE 2.—The results of Bernoulli analyses I–IV. *K* is the number of estimated model parameters, deviance is -2 times the maximized log-likelihood, AIC_c is the 2nd-order corrected Akaike information criterion, and *w* is the Akaike weight. Bernoulli analysis I: for all 104 births, of which 46 were male, M_0 models these data as an unbiased Bernoulli trial; and M_1 as a biased Bernoulli trial. Bernoulli analysis II: for the 88 births, of which 41 were male, that constitute the 1st through 5th births of females that first calved in the study, models M_0 and M_1 are as in Bernoulli analysis I, M_2 models 1st births and subsequent births as independent Bernoulli trials; M_3 models 1st births as a Bernoulli trial and subsequent births as independent Bernoulli trials depending on the sex of the prior birth; and M_4 models the births of each order, 1 through 5, as independent Bernoulli trials. Bernoulli analysis III: models M_0 , M_1 , and M_3 are as in Bernoulli analysis II for the 102 births, of which 46 were male, that exclude just the 1st births (both female) of the 2 females imported as adults. Bernoulli analysis IV: models M_0 and M_1 are as in Bernoulli analysis I applied to the cumulative birth sex ratio of 23:37 through 2004.

Analysis	Model	Deviance	<i>K</i>	ΔAIC_c	<i>w</i>
I	M_0	6.475	0	0	0.567
	M_1	5.087	1	0.612	0.410
II	M_0	5.339	0	0	0.679
	M_1	4.930	1	1.637	0.300
	M_2	8.291	2	7.093	0.020
	M_3	11.449	3	12.395	0.001
	M_4	16.177	5	21.570	0.000
III	M_0	6.054	0	0	0.628
	M_1	5.074	1	1.058	0.370
	M_3	11.818	3	12.009	0.002
IV	M_0	7.796	0	1.228	0.351
	M_1	4.499	1	0	0.649

any (Table 4). The regression coefficient for PriorRain7 was consistently negative across all models in which it appeared, whereas those for maternal age and population size were consistently positive across models; those of the remaining predictors did not have consistent sign across models. Neither interactions between fixed effects nor modeling maternal age nonlinearly using generalized additive mixed models provided improvements over the top-ranked, more-parsimonious, models, for example, the best such model consisted of the interaction between PriorRain7 and population size with a ΔAIC_c value of 3.34.

The model-averaged means across all 32 models of the variances of maternal identity and year of conception were 0.30 and 0.064, respectively. The value 0.30 corresponds to a repeatability on the latent scale, a measure of the contribution of the random factor to the variance unaccounted for by the fixed effects (Nakagawa and Schielzeth 2010), of 8.4%. The intercept of the base model corresponds to a probability that differs from the observed BSR of the BS89 data by less than 0.002.

For Bernoulli analysis II, only models M_0 and M_1 , unbiased and biased Bernoulli trials of constant probability of male birth sex, respectively, received compelling support (Table 2); the evidence ratio of M_0 to M_1 was 2.26 for this subset of the data. Although the sample sizes for 6th- and 7th-order births were small, because they consisted exclusively of female births we

TABLE 3.—Second-order corrected Akaike information criterion (AIC_c) ranking for the logistic regression modeling of BS89 data for those models with $\Delta AIC_c \leq 3$ and the global model (Global) with all 5 fixed effects and the 2 random effects of maternal identity and year of conception. Base is the model without fixed effects but with the 2 random effects. PR7 is PriorRain7; GR is cumulative rainfall during gestation; MaC is maternal age at conception; and PopSize is population size and ASR is adult sex ratio, both at conception. *K* is the number of estimated model parameters, deviance is -2 times the maximized log-likelihood, and *w* is the Akaike weight.

Model	<i>K</i>	Deviance	ΔAIC_c	<i>w</i>
Base	3	122.0	0	0.149
PR7	4	120.4	0.594	0.111
PopSize	4	121.4	1.594	0.067
MaC	4	121.4	1.594	0.067
PR7+PopSize	5	119.2	1.641	0.066
GR	4	121.9	2.094	0.052
PR7+MaC	5	119.7	2.141	0.051
ASR	4	122.0	2.194	0.050
PR7+GR	5	120.3	2.741	0.038
PR7+ASR	5	120.4	2.841	0.036
Global	8	118.7	8.218	0.002

repeated this analysis using all births through order 7. The numerical values displayed in Table 2 changed only slightly and did not alter the conclusions. The results of Bernoulli analysis III were similar to those of II (Table 2), although the evidence ratio for M_0 to M_1 was reduced to 1.70, closer to that of Bernoulli analysis I.

The cumulative BSRs over time were female biased for each year, although varied nonmonotonically, with the cumulative BSR through 2004 of 23:37 the only one for which the 1-sided binomial test for an unbiased binomial trial rejected the null hypothesis (Table 1). For Bernoulli analysis IV, model M_1 was ranked as top model, with evidence ratio 1.8 compared to model M_0 (Table 2). The maximum-likelihood value of the probability θ of male birth according to M_1 was 0.383; the model-averaged value was 0.424 with unconditional *SE* of 0.084.

DISCUSSION

Owen-Smith (1988) reported a perinatal sex ratio for black rhinoceros from published records of fetuses and newborn calves for both wild and captive populations of approximately 122 males per 100 females (0.550), for which the 95% binomial confidence interval (Zar 1999) is [0.482, 0.616]. The SKKR BSR (0.442) falls outside this interval suggesting that it may be unusual. The model-averaged BSR of Bernoulli analysis I (0.476 ± 0.057), however, indicates that the observed BSR may be interpretable as stochastic variation about a BSR compatible with Owen-Smith's (1988) data.

Although a lack of bias in the observed population BSR does not preclude variation in sex allocation at some other scale, no logistic regression model with fixed effects outperformed the base model. The fixed effect with most evidence for some influence on birth sex was the measure of rain prior to

TABLE 4.—Relative importance (RI) of fixed effects over all 32 logistic regression models and their standardized regression coefficients and standard errors (*SE*) in the global model. Fixed effects are as in Table 3.

Predictor	RI	$\bar{X} \pm SE$
PR7	0.444	-0.40 ± 0.26
PopSize	0.327	0.28 ± 0.27
MaC	0.301	0.15 ± 0.24
GR	0.251	-0.05 ± 0.24
ASR	0.246	-0.09 ± 0.25

conception, but the effect was not convincing. The random factors of maternal identity and year of conception were unimportant. We therefore conservatively concluded that the logistic regression modeling provided no compelling evidence for any influence of the effects, fixed or random, on birth sex (similar to Visscher et al. 2004).

Rainfall is likely a poor indicator of individual maternal condition, except possibly in relation to seasonal or annual variation. The negative coefficient obtained in our models is counterintuitive, but no evidence supports a meaningful biological interpretation. If rainfall prior to conception influences maternal state at conception by enhancing maternal investment potential, its influence on sex allocation may be undermined in black rhinoceros because differences in maternal condition may have to be pronounced for black rhinoceros to favor biased sex allocation to males; the time from weaning to sexual maturity for males may be too long for mothers to influence their reproductive success (Green and Rothstein 1991); or lengthy gestation may reduce the importance of maternal condition at conception as a predictor of the potential investment during lactation (West 2009). On the other hand, Schwanz et al. (2006) concluded that any component of offspring reproductive value is a potential target for maternal investment leading to biased sex ratios, including juvenile survival, and not just adult fecundity. However, rainfall may just be a poor covariate for maternal state and direct measures of primary productivity, such as the normalized differential vegetation index, may outperform rainfall in explaining demographic responses, including maternal state, to ecological conditions (Rasmussen et al. 2006).

Our study did not address the Trivers–Willard hypothesis itself. The relevance of the Trivers–Willard hypothesis to black rhinoceros in general, and the SKKR population in particular, remains uncertain. This issue is particularly challenging if it is relative differences in maternal condition (Schwanz et al. 2010) or the relative numbers in different states of condition (Schwanz et al. 2006) at conception that underpins the Trivers–Willard hypothesis.

Population size manifested no compelling effect despite the population's expansion throughout the study, although its coefficient was positive in the logistic regression models, as expected from the local resource competition hypothesis. Weladji and Laflamme-Mayer (2011) reported that the probability of male birth increased (which they attributed to a local resource competition effect) for a population of black

rhinoceros that increased in size from about 50 to about 85 over 37 years in a reserve about 1.7 times larger than SKKR and thus at a slower rate of growth and at lower mean density. We previously found that population size had no effect on adult female reproduction for the SKKR population (Law et al. 2013), indicating an absence of resource limitation, consistent with van Lieverloo et al. (2009). Hence, the conditions required for a local resource competition effect apparently did not exist for the SKKR population. It is unknown how close the SKKR population may have come to carrying capacity by the end of 2008, at which time mean density was 0.5 individuals/km². Reported average densities for black rhinoceros are typically < 0.5 individuals/km² but may be 3 times higher in good habitat (Owen-Smith 1988).

Maternal age was not a compelling influence, despite a positive coefficient over all models. Although maternal age (at conception) ranged from about 3.5 to 30 years, the mean $\pm SD$ was 10.8 ± 5.3 years. The SKKR population was still a young population, so older ages were not well represented, and prime-aged mothers of age 10–25 years dominated the distribution of maternal age only toward the end of the study. The BSR for all SKKR mothers aged < 10 years was 27:31, aged 10–24 years was 17:27, and ≥ 25 years was 2:0 (the only dependence on intervals of uncertainty was that 1 calf of each sex in the prime-aged interval may belong to the earlier interval and 1 male to the later interval). These data do not conform to Saltz's (2001) prediction of a male bias for prime-aged ungulates; nor did nonlinear dependencies of the logit of birth sex on maternal age perform well in the modeling.

Rainfall during gestation and adult sex ratio were the least-supported fixed effects (Table 4), and their regression coefficients had varying sign across models. For their study, Weladji and Laflamme-Mayer (2011) reported that the likelihood of male birth increased with increasing rainfall during gestation, which ranged from a similar minimum value but to nearly twice the maximum that occurred for the SKKR population. Perhaps such extreme variation is required to elicit a response in sex allocation.

Bernoulli analyses II and III provided no evidence that birth sex depended upon primiparity (of 26 firstborn, 11 were males and 15 were females), birth order in general, or sex of the previous birth, the last contrary to the study of Hrabar and du Toit (2005). Other measures of maternal reproductive status that might influence sex allocation include lactation, which may influence maternal condition at conception or during gestation (Côté and Festa-Bianchet 2001; Visscher et al. 2004), and interbirthing interval. We had no direct information on lactation status for SKKR females, but interbirthing interval did not differentiate birth sex in the SKKR population (the mean $\pm SD$ was 28.4 ± 5.1 months [$n = 38$] and 28.5 ± 6.9 months [$n = 35$] for interbirthing intervals that terminated in female birth and male birth, respectively).

We detected no influence on sex allocation from rainfall, population size, maternal age, adult sex ratio, or female reproductive status in the SKKR population. If black rhinoceros facultatively adjust sex allocation, either we failed

to detect it at the appropriate scale in SKKR or the conditions that elicit it did not pertain. The quality of the habitat, lack of extreme environmental conditions, and underrepresentation of older females during the study are compatible with the latter possibility. Understanding sex allocation in the black rhinoceros, which inhabits a wide range of habitats, will require studies across that range, from the most favorable to most extreme, as well as across ranges of density. The consistent female bias in cumulative BSR over the years remains a tantalizing fact and through 2004 was better modeled as a biased Bernoulli trial rather than an unbiased one. On the other hand, the actual number of males and females born each year (easily computed from Table 1) is less compelling evidence against birth sex resulting from an unbiased Bernoulli trial, as expected by chromosomal sex determination. The possibility of temporary female bias in birth sex during early stages of expansion after reintroduction or due to perturbation of age structure by intense poaching (West and Godfray 1997) would be favorable for the management and recovery of black rhinoceros and deserves further investigation.

ACKNOWLEDGMENTS

Our collaboration is a by-product of an International Science Liaison Foreign Fellowship, National Research Foundation, Republic of South Africa, that PRL shared with W. Linklater in 2005. We thank W. Linklater, for his pivotal role in obtaining this fellowship, bringing the 3 authors together, and for ongoing dialogue on rhinos; G. Kerley, for hosting W. Linklater and PRL during their fellowship at the Centre for African Conservation Ecology, Nelson Mandela Metropolitan University; the SKKR field rangers; and reviewers, including M. Festa-Bianchet, for suggestions that improved the manuscript.

SUPPORTING INFORMATION

SUPPORTING INFORMATION S1.—Raw data; details relating the population sex ratio to the birth sex ratio; specific values of U employed in BF's quantification of uncertainty of birth and death dates; details of rainfall; details on the goodness-of-fit tests for the global model of the logistic regression; results for the BS103 data set; and likelihoods for Bernoulli analyses I–IV.

Found at DOI: 10.1644/13-MAMM-A-175.S1

LITERATURE CITED

- BERKELEY, E. V., AND W. L. LINKLATER. 2010. Annual and seasonal rainfall may influence progeny sex ratio in the black rhinoceros. *South African Journal of Wildlife Research* 40:53–57.
- BURNHAM, K. P., AND D. R. ANDERSON. 2002. Model selection and multimodel inference: a practical information-theoretic approach. 2nd ed. Springer-Verlag, New York.
- CAMERON, E. Z. 2004. Facultative adjustment of mammalian sex ratios in support of the Trivers–Willard hypothesis: evidence for a mechanism. *Proceedings of the Royal Society of London, B. Biological Sciences* 271:1723–1728.
- CAMERON, E. Z., P. R. LEMONS, P. W. BATEMAN, AND N. C. BENNETT. 2008. Experimental alteration of litter sex ratios in a mammal. *Proceedings of the Royal Society of London B. Biological Sciences* 275:323–327.
- CAMERON, E. Z., AND W. L. LINKLATER. 2007. Extreme sex ratio variation in relation to change in condition around gestation. *Biology Letters* 3:395–397.
- CAMERON, E. Z., W. L. LINKLATER, K. J. STAFFORD, AND E. O. MINOT. 2000. Aging and improving reproductive success in horses: declining reproductive value or just older and wiser? *Behavioral Ecology and Sociobiology* 47:243–249.
- CHARLESWORTH, B. 1994. *Evolution in age-structured populations*. 2nd ed. Cambridge University Press, Cambridge, United Kingdom.
- CHARNOV, E. L. 1982. *Sex allocation*. Princeton University Press, Princeton, New Jersey.
- COCKBURN, A., S. LEGGE, AND M. C. DOUBLE. 2002. Sex ratios in birds and mammals: can the hypotheses be disentangled? Pp. 266–286 in *Sex ratios: concepts and research methods* (I. C. W. Hardy, ed.). Cambridge University Press, Cambridge, United Kingdom.
- CONVERSE, S. J., G. C. WHITE, AND W. M. BLOCK. 2006. Small mammal responses to thinning and wildfire in ponderosa pine-dominated forests of the southwestern United States. *Journal of Wildlife Management* 70:1711–1722.
- CÔTÉ, S. D., AND M. FESTA-BIANCHET. 2001. Offspring sex ratio in relation to maternal age and social rank in mountain goats (*Oreamnos americanus*). *Behavioral Ecology and Sociobiology* 49:260–265.
- DOHERTY, P. F., G. C. WHITE, AND K. P. BURNHAM. 2012. Comparison of model building and selection strategies. *Journal of Ornithology* 152, supplement 2:S317–S323.
- EMSLIE, R. H., K. ADCOCK, AND H. B. HANSEN. 1995. Fine tuning the Rhino Management Group age class system. Rhino Management Group, Rhino Resource Center, www.rhinoresourcecenter.com. Accessed February 11, 2014.
- FESTA-BIANCHET, M. 1996. Offspring sex ratio studies of mammals: does publication depend upon quality of the research or direction of the results? *Écoscience* 3:42–44.
- FIKE, B. 2011. The demography and population dynamics of a reintroduced black rhinoceros population on the Great Fish River Reserve, Eastern Cape Province. M.S. thesis, Rhodes University, Grahamstown, South Africa.
- FRANK, S. A. 1987. Individual and population sex allocation patterns. *Theoretical Population Biology* 31:47–74.
- FRANK, S. A. 1998. *Foundations of social evolution*. Princeton University Press, Princeton, New Jersey.
- GANQA, N. M., P. F. SCOGINGS, AND J. G. RAATS. 2005. Diet selection and forage quality factors affecting woody plant selection by black rhinoceros in the Great Fish River Reserve, South Africa. *South African Journal of Wildlife Research* 35:77–83.
- GARNIER, J. N., M. W. BRUFORD, AND B. GOOSENS. 2001. Mating system and reproductive skew in the black rhinoceros. *Molecular Ecology* 10:2031–2041.
- GARROWAY, C. J., AND H. G. BRODERS. 2007. Adjustment of reproductive investment and offspring sex ratio in white-tailed deer (*Odocoileus virginianus*) in relation to winter severity. *Journal of Mammalogy* 88:1305–1311.
- GELMAN, A., AND J. HILL. 2007. *Data analysis using regression and multilevel/hierarchical models*. Cambridge University Press, Cambridge, United Kingdom.
- GREEN, W. C. H., AND A. ROTHSTEIN. 1991. Sex bias or equal opportunity? Patterns of maternal investment in bison. *Behavioral Ecology and Sociobiology* 29:373–384.
- HARDY, I. C. W. (ed.). 2002. *Sex ratios: concepts and research methods*. Cambridge University Press, Cambridge, United Kingdom.

- HELLE, S., T. LAAKSONEN, A. ADAMSSON, J. PARANKOS, AND O. HUITU. 2008. Female field voles with high testosterone and glucose levels produce male-biased litters. *Animal Behaviour* 75:1031–1039.
- HEWISON, A. J., J.-M. GALLARD, P. BLANCHARD, AND M. FESTA-BIANCHET. 2002. Maternal age is not a predominant determinant of progeny sex ratio variation in ungulates. *Oikos* 98:334–339.
- HOGG, J. T., C. C. HASS, AND D. A. JENNI. 1992. Sex-biased maternal expenditure in Rocky Mountain bighorn sheep. *Behavioral Ecology and Sociobiology* 31:243–251.
- HOSMER, D. W., AND S. LEMESHOW. 2000. Applied logistic regression. 2nd ed. Wiley Inter-Science, New York.
- HRABAR, H., AND J. T. DU TOIT. 2005. Dynamics of a protected black rhino (*Diceros bicornis*) population: Pilanesberg National Park, South Africa. *Animal Conservation* 8:259–267.
- ISAAC, J. L., A. K. KROCKENBERGER, AND C. N. JOHNSON. 2005. Adaptive sex allocation in relation to life-history in the common brushtail possum *Tichosurus vulpecula*. *Journal of Animal Ecology* 74:552–558.
- KOJOLA, I. 1998. Sex ratio and maternal investment in ungulates. *Oikos* 83:567–573.
- KRACKOW, S. 2002. Why parental sex ratio manipulation is rare in higher vertebrates. *Ethology* 108:1041–1056.
- KRUK, L. E. B., T. H. CLUTTON-BROCK, S. D. ALBON, J. M. PEMBERTON, AND F. E. GUINNESS. 1999. Population density affects sex ratio variation in red deer. *Nature* 399:459–461.
- LAW, P. R., B. FIKE, AND P. C. LENT. 2013. Mortality and female fecundity in an expanding black rhinoceros (*Diceros bicornis minor*) population. *European Journal of Wildlife Research* 59:477–485.
- LEIMAR, O. 1996. Life-history analysis of the Trivers and Willard sex-ratio problem. *Behavioral Ecology* 7:316–325.
- LENT, P. C., AND B. FIKE. 2003. Home ranges, movements and spatial relationships in an expanding population of black rhinoceros in the Great Fish River Reserve, South Africa. *South African Journal of Wildlife Research* 33:109–118.
- LINKLATER, W. L. 2007. Translocation reverses birth sex ratio depending on its timing during gestation: evidence for the action of two sex-allocation mechanisms. *Reproduction, Fertility and Development* 19:831–839.
- MARTIN, J. G. A., AND M. FESTA-BIANCHET. 2011. Sex ratio bias and reproductive strategies: what sex to produce when? *Ecology* 92:441–449.
- MYSTERUD, A., N. G. YOCOZ, N. C. STENSETH, AND R. LANGVATN. 2000. Relationship between sex ratio, climate and density in red deer: the importance of spatial scale. *Journal of Animal Ecology* 69:959–974.
- NAKAGAWA, S., AND H. SCHIELZETH. 2010. Repeatability for Gaussian and non-Gaussian data: a practical guide for biologists. *Biological Reviews* 85:935–956.
- OWEN-SMITH, R. N. 1988. Megaherbivores: the influence of very large body size on ecology. Cambridge University Press, Cambridge, United Kingdom.
- PEN, I., AND F. J. WEISSING. 2002. Optimal sex allocation: steps towards a mechanistic theory. Pp. 26–45 in *Sex ratios: concepts and research methods* (I. C. W. Hardy, ed.). Cambridge University Press, Cambridge, United Kingdom.
- PROFFITT, K. M., R. A. GARROTT, AND J. J. ROTELLA. 2008. Variation in offspring sex ratio among individual Weddell seal (*Leptonychotes weddellii*) females of different quality. *Behavioral Ecology and Sociobiology* 62:1679–1687.
- RASMUSSEN, H. B., G. WITTEMYER, AND I. DOUGLAS-HAMILTON. 2006. Predicting time-specific changes in demographic processes using remote-sensing data. *Journal of Applied Ecology* 43:366–376.
- R DEVELOPMENT CORE TEAM. 2009. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. www.R-project.org.
- ROCHE, J. R., J. M. LEE, AND D. P. BERRY. 2006. Pre-conception energy balance and secondary sex ratio—partial support for the Trivers–Willard hypothesis in dairy cows. *Journal of Dairy Science* 89:2119–2125.
- SALTZ, D. 2001. Progeny sex ratio variation in ungulates: maternal age meets environmental perturbation of demography. *Oikos* 94:377–384.
- SALTZ, D., AND P. KOTLER. 2003. Maternal age is a predominant determinant of progeny sex ratio variation in ungulates: a reply to Hewison et al. *Oikos* 101:646–648.
- SCHWANZ, L. E., J. G. BAGG, AND E. L. CHARNOV. 2006. Maternal condition and facultative sex ratios in populations with overlapping generations. *American Naturalist* 168:521–530.
- SCHWANZ, L. E., F. J. JANZEN, AND S. R. PROULX. 2010. Sex allocation based on relative and absolute condition. *Evolution* 64:1331–1345.
- SHELDON, B. C., AND S. A. WEST. 2004. Maternal dominance, maternal condition, and offspring sex ratio in ungulate mammals. *American Naturalist* 163:40–54.
- SHORROCKS, B. 2007. The biology of African savannahs. Oxford University Press, Oxford, United Kingdom.
- TRIMBLE, M. J., S. M. FERREIRA, AND R. J. VAN AARDE. 2009. Drivers of megaherbivore demographic fluctuations: inference from elephants. *Journal of Zoology (London)* 279:18–26.
- VAN HOOFT, P., ET AL. 2010. Rainfall-driven sex-ratio genes in African buffalo suggested by correlations between Y-chromosomal haplotype frequencies and foetal sex ratio. *BMC Evolutionary Biology* 10:106.
- VAN LIEVERLOO, R. J., ET AL. 2009. A comparison of faecal analysis with backtracking to determine the diet composition and species preference of the black rhinoceros (*Diceros bicornis minor*). *European Journal of Wildlife Research* 55:505–515.
- VISSCHER, D. R., R. J. VAN AARDE, AND I. WHYTE. 2004. Environmental and maternal correlates of foetal sex ratios in African buffalo (*Syncerus caffer*) and savanna elephant (*Loxodonta africana*). *Journal of Zoology (London)* 264:111–116.
- WELADJI, R. B., AND K. LAFLAMME-MAYER. 2011. Influence of environmental conditions on sex allocation in the black rhinoceros population of Mkhuze Game Reserve, South Africa. *African Journal of Ecology* 49:471–480.
- WEST, S. A. 2009. Sex allocation. Princeton University Press, Princeton, New Jersey.
- WEST, S. A., AND H. C. J. GODFRAY. 1997. Sex ratio strategies after perturbation of the stable age distribution. *Journal of Theoretical Biology* 186:213–221.
- WILD, G., AND S. A. WEST. 2007. A sex allocation theory for vertebrates: combining local resource competition and condition-dependent allocation. *American Naturalist* 170:E112–E128.
- WILLIAMS, B. K., J. D. NICHOLS, AND M. J. CONROY. 2002. Analysis and management of animal populations. Academic Press, San Diego, California.
- ZAR, J. H. 1999. Biostatistical analysis. 4th ed. Prentice Hall, Upper Saddle River, New Jersey.
- ZUUR, A. F., E. N. IENO, N. J. WALKER, A. A. SAVELIEV, AND G. M. SMITH. 2009. Mixed effects models and extensions in ecology with R. Springer-Verlag, New York.

Submitted 19 July 2013. Accepted 3 December 2013.

Associate Editor was Christine R. Maher.

Supporting Information S1 for 'Birth sex in an expanding black rhinoceros (*Diceros bicornis minor*) population' by Law, Fike, and Lent.

Population Sex Ratio and Birth Sex Ratio

The SKKR population was founded with the release in June, 1986, of one adult female (aged about 24), one subadult (SA) female (aged about three), and two males, both judged to be adults. One of the males died in 1988 from an injury that occurred prior to importation and was treated as a failed import.

In 1989, a second cohort was released consisting of three SA females and three SA males; one female and one male died in 1989 and another male died in 1990, each regarded as a failed import. In November, 1990, when the population was eight, two adult females (one aged about 15; the other aged about 7 and pregnant) and a SA male were imported. The pregnant female calved in December 1990 but both mother and calf were dead by the end of 1991 and are treated as failed imports. In January 1992, when the population was 11, a female SA and a male adult were released. Between September 1997, when the population was 26, and December 1997, a cohort of 7 females and 6 males, all SAs and all quite young (about three years of age) except one (aged about six) was imported.

In summary, 13 males and 15 females were introduced but 3 males and 2 females died soon after release and did not contribute to the population. The surviving imports included only two females and two males that were already adults. One further female adult entered the SKKR population, from the eastern sector of the GFRR, in 2003. This immigrant was the only exception to the demographic isolation of the SKKR population during the study period.

The export of 1 SA male and 4 SA females in 2006 yielded a sex ratio of 9:10 as a result of imports and exports, after discounting the failed imports. One unsexed calf and 7 rhino of each sex died during the study period. The population sex ratio at the end of 2008 was 48:62 (43.6% male), and this apparent female bias therefore derives almost exclusively from the birth-sex record of the SKKR population. The 106 births during the study period included the unsexed calf that died within a year of its birth and 1 female that was first observed as a subadult after the end of the study and its mother never identified. These 2 calves are excluded from our study (except for their contribution to population size). The remaining 104 birth sexes constituted our study population, with sex ratio 46:58 (44.2% male; whence the exclusion of the female with unknown mother is a conservative tactic). Six births (2:4) occurred to females imported into SKKR as mature females with unknown previous reproductive history. The remaining 98 births were organized into birth sequences of mothers (Table S1). Inter-birthing intervals (IBIs) of the SKKR population were studied in Law et al. (2013). Only 3 birth sequences contained an IBI of sufficient length to raise the question of unobserved births but there was no other evidence to suggest that such had occurred (the female subadult discovered after the end of the study period could not be

credibly assigned as a previously unknown calf to any of these birth sequences) and we took the recorded birth order as accurate and complete.

Table S1. The 105 birth sexes presented in their birth sequences, organized by length (N) of the sequence; the birth sequences of the 2 females imported as mature adults appear in the final cell as their prior calves are unknown in both number and sex, ‘u’ refers to the sole unsexed birth.

N	Birth sequences
9	FMFFFFFFMM
8	FFMFFFFFFM
7	FFFMMFF
6	MFFFMF
5	MMMFM; FFFMM; FFMMF
4	MMMM; MFMF; MMFF; MMFM; FFFF
3	FFM; MFF; FMM; FMF; MMM; MMM; MFF
2	FF; FM; FM; FF; MM
1	F; F
-	FFFu; FMM

Intervals of Uncertainty for Birth Dates

The values of U employed by Fike (2011) were: $U = 0$ (uncertainty in the nominal date at most 1 week); $U = 1$; $U = 3$; $U = 6$; $U = 12$; $U > 12$. For the 104 births, 23 had $U = 0$, 37 had $U = 1$, 29 had $U = 3$, 14 had $U = 6$, 1 had $U = 12$, and none had $U > 12$.

Precipitation

Following several other studies (Visscher et al. 2004; Hrabar and du Toit 2005; van Hooft et al. 2010; Berkeley and Linklater 2011; Weladji and Laflamme-Mayer 2011), we intended to employ a measure of rainfall prior to conception as an indicator of a component

of maternal state and cumulative rainfall during gestation as an indicator of adverse conditions on the secondary sex ratio (Kruuk et al. 1999; Garroway and Broders 2007; Weladji and Laflamme-Mayer 2011).

Single wet and dry seasons are typical of southern Africa (Shorrocks 2007). We used a monthly rainfall figure that was a mean from 3 locations in SKKR and defined the dry season as May–September, inclusive, the wet season as October–April, inclusive, and a seasonal year as a dry season followed by a wet season (see Law et al. 2013 for details). For the 23 seasonal years beginning in May 1986, the mean annual precipitation was 452 mm (range, 253–609; CV = 18%); mean monthly rainfall for dry season months was 21 mm (range, 0–168; CV = 123%) and for wet season months was 49 mm (range, 1–194; CV = 71%). Table S2 indicates precipitation over the years of the study.

TABLE S2. Wet (W), Normal (N), and Dry (D) years. We called a year normal (N) if the annual rainfall was within 1 SD of the mean, wet (W) if wetter than this range, and dry (D) if drier than this range. The n 'th seasonal year began in May of the calendar year 1986 + n and ended in April of the following year.

Seasonal Year	0	1	2	3	4	5
	D	N	N	N	D	N
Seasonal Year	6	7	8	9	10	11
	D	W	N	N	N	N
Seasonal Year	12	13	14	15	16	17
	N	N	N	N	W	D
Seasonal Year	18	19	20	21	22	
	N	N	W	N	N	

Fixed-Effect Variables for Logistic Regression Modelling

TABLE S3. Summary statistics for the fixed effects for the logistic regression modelling for the datasets BS89 and BS103. PriorRain7 is the cumulative rainfall (mm) over the 7 month period ending with the month of conception; RainGest is cumulative rainfall (mm) during gestation; MaC is maternal age (in months), PopSize is population size, and ASR is adult sex ratio (M/(M+F), all measured at conception; PriorRain12 is the cumulative rainfall (mm) for the 12 month period ending with the month of conception; PriorRain24 is the cumulative rainfall (mm) over the 12 month period prior to that of PriorRain12.

BS89	range	mean \pm SD	BS103	range	mean \pm SD
PriorRain7	[103, 419]	271 \pm 84	PriorRain12	[265, 694]	472 \pm 92
RainGest	[348, 767]	580 \pm 90	PriorRain24	[301, 624]	453 \pm 76
PopSize	[3, 97]	58 \pm 28	PopSize	[3, 97]	57 \pm 27
MaC	[43, 365]	130 \pm 64	MaC	[43, 365]	130 \pm 64
ASR	[0.2,0.5]	0.368 \pm 0.056	ASR	[0.2, 0.67]	0.368 \pm 0.062

Goodness-of-Fit Results for Logistic Regression Modelling

We followed the recommendation of Hosmer and Lemeshow (2000:162–163) to employ a combination of tests to assess both calibration (fit to data) and discrimination (between the sexes) of our global model. For calibration, we performed the Hosmer-Lemeshow test based on grouping the predicted values into deciles (Hosmer and Lemeshow 2000) and the le Cessie-van Houwelingen(-Copas-Hosmer unweighted-sum-of-squares) test (le Cessie and van Houwelingen 1991). These tests were performed using function HLgof.test in R package MKmisc. We first assessed discrimination by assigning male birth sex if a predicted value was at least 0.5 and comparing with observed values and then, more generally, by computing the area under the receiver operating curve (using function colAUC in R package caTools). The le Cessie-van Houwelingen test requires specification of a model with continuous covariates so we conducted this test for the model with the 5 fixed effects only (i.e., no random effects, using function glm in R), as in Proffitt et al. (2008). The other tests required only the list of pairs of observed and fitted values, so we performed each of them using the fitted values returned by both functions lmer and glm, i.e., for the global model with and without random factors, respectively.

The tests of calibration of the global logistic-regression model for the BS89 dataset indicated the fitted values of the global GLM model were consistent with the data while the fitted values returned by lmer for the global GLMM model were marginally consistent with the data (Table S4). Yet the global GLMM had better discrimination ('acceptable' as judged by the AUC-ROC statistic; Hosmer and Lemeshow 2000:162) than the global GLM. The poorer calibration of the GLMM fitted values resulted because neither model assigned high probabilities to any male birth. All fitted values were less than 0.67 and 0.59 for the GLMM and GLM global models, respectively, so the improved specificity of the GLMM over the GLM decreased the calibration (Table S4).

TABLE S4. Goodness of fit of the global model to the BS89 data. GLM refers to the logistic regression with the 5 fixed effects but no random effects, GLMM to the mixed model with the 5 fixed effects and 2 random effects. XY is the number of births of sex X to which the model assigns a sex of Y under the rule: predicted probability of at least 0.5 is assigned a birth sex of male; classification success = (MM+FF)/(no. observations); specificity = MM/(no. male births); sensitivity = FF/(no. female births); AUC-ROC is area under the receiver operating curve.

	BS89 GLM	BS89 GLMM	BS103 GLM	BS103 GLMM
Hosmer-Lemeshow p	0.20	0.07	0.32	0.02
Le Cessie-van Houwelingen p	0.11	na	0.38	na
FM	11	8	14	8
FF	38	41	43	49
MM	20	23	18	27
MF	20	17	28	19
Classification success	65%	72%	59%	74%
Specificity	50%	58%	39%	59%
Sensitivity	78%	84%	75%	86%
AUC-ROC	0.62	0.78	0.59	0.77

Results for BS103 Dataset

TABLE S5. AIC_c ranking for the logistic regression modelling of the BS103 dataset. PR12 is PriorRain12; PR24 is PriorRain 24; MaC is maternal age at conception; PopSize is population size and ASR adult sex ratio, both at conception; Base is the model without fixed effects but with the two random effects of maternal identity and year of conception; Global is the model with all five fixed effects and the two random effects; K is the number of estimated model parameters, deviance is -2 times the maximized log-likelihood, w is the Akaike weight.

Model	K	deviance	ΔAIC_c	w
Base	3	141.2	0	0.154
PR12	4	139.7	0.666	0.111
PopSize	4	140.3	1.266	0.082
PR12+	5	138.4	1.576	0.070
PopSize				
MaC	4	141.1	2.066	0.055
PR24	4	141.2	2.166	0.052
ASR	4	141.2	2.166	0.052
PR12+	5	139.5	2.676	0.041
MaC				
PR12+	5	139.7	2.876	0.037
PR24				
PR12+	5	139.7	2.876	0.037
ASR				
Global	8	138.3	8.389	0.002

TABLE S6. Relative importance (RI) of predictors for BS103 with their standardized regression coefficients and their standard errors (SE) for the global model; predictors denoted as in Table S5.

Fixed Effect	RI	Mean \pm SE
PR12	0.431	-0.31 \pm 0.22
PopSize	0.359	0.26 \pm 0.23
MaC	0.258	0.05 \pm 0.22
ASR	0.249	-0.05 \pm 0.21
PR24	0.247	-0.00 \pm 0.21

Likelihood Models for Bernoulli Analyses I – IV

In the models described below, ${}^n C_r$ denotes the binomial coefficient $\frac{n!}{(n-r)!r!}$

Bernoulli Analysis I:

The data are $n = 104$ births, of which $M = 46$ were male. The likelihood for the model M_0 of these data as an unbiased Bernoulli trial is

$$L_0 = {}^n C_M (1/2)^n.$$

The likelihood for the model M_1 of these data as a biased Bernoulli trial is

$$L_1 = {}^n C_M \vartheta^M (1-\vartheta)^{n-M}.$$

Model M_0 has no model parameters; the ML value of ϑ in M_1 is 46/104.

Bernoulli Analysis II:

The number of (male,female) births for birth order 1 through 5 were (11,15), (12,12), (9,10), (5,7), and (4,3), totalling 88 births, of which 41 were male. Models M_0 and M_1 are of the same form as above, whence the likelihoods are L_0 and L_1 , but for the present data. The ML estimate of the parameter ϑ in M_1 is 41/88. For model M_2 , the likelihood is

$$L_2 = [{}^{26} C_{11} \pi^{11} (1-\pi)^{26}] \cdot [{}^{62} C_{30} \tau^{30} (1-\tau)^{32}];$$

the ML estimates of π and τ are 11/26 and 30/62, respectively. For M_3 , note that for births of 2nd through 5th order, of the 28 preceded by a male birth, 16 were male births, while of the 34 preceded by a female birth, 14 were male births. The likelihood for M_3 is therefore

$$L_3 = [{}^{26} C_{11} \pi^{11} (1-\pi)^{15}] \cdot [{}^{28} C_{16} \chi^{16} (1-\chi)^{12}] \cdot [{}^{34} C_{14} \varphi^{14} (1-\varphi)^{20}];$$

the ML estimates of π , χ , and φ are 11/26, 16/28, and 14/34, respectively. Finally, for model M_4 , the likelihood is

$L_4 = [{}^{26}C_{11} \pi^{11} (1-\pi)^{15}] \cdot [{}^{24}C_{12} \alpha^{12} (1-\alpha)^{12}] \cdot [{}^{19}C_9 \beta^9 (1-\beta)^{10}] \cdot [{}^{12}C_5 \gamma^5 (1-\gamma)^7] \cdot [{}^7C_4 \delta^4 (1-\delta)^3]$;
The ML estimates of π , α , β , γ , and δ are 11/26, 12/24, 9/19, 5/12, and 4/7, respectively.

Bernoulli Analysis III:

The data consist of 102 births: 11 male and 15 female 1st-borns; 18 males and 14 females born successive to a male birth; 17 males and 27 females born successive to a female birth. The models M_0 , M_1 , and M_3 are as in Analysis III, but applied to these data, so the likelihoods are L_0 and L_1 , with $n = 102$ and $M = 46$, while

$$L_3 = [{}^{26}C_{11} \pi^{11} (1-\pi)^{15}] \cdot [{}^{32}C_{18} \chi^{18} (1-\chi)^{14}] \cdot [{}^{44}C_{17} \varphi^{17} (1-\varphi)^{27}]$$

the ML estimates of π , χ , and φ are 11/26, 18/32, and 17/44, respectively.

Bernoulli Analysis IV:

Models M_0 and M_1 as in Analysis I but for the data $n = 60$, $M = 23$.

Literature Cited

LE CESSIE, S. AND J. C. VAN HOUWELINGEN. 1991. A goodness-of-fit Test for Binary Regression Models, Based on Smoothing Methods. *Biometrics* 47:1267–1282.