

Environmental and maternal correlates of foetal sex ratios in the African buffalo (*Syncerus caffer*) and savanna elephant (*Loxodonta africana*)

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(Accepted 26 January 2004)

Abstract

Many species exhibit skewed sex ratios at birth. Here we investigate the relationships between environmental and maternal variables (as surrogates for maternal condition) and foetal sex in African buffalo *Syncerus caffer* and elephant *Loxodonta africana* of the Kruger National Park, South Africa. Using logistic regression no significant effect was found of year, maternal lactational status, maternal age, rainfall or density on foetal sex ratio. Using a subset of our data, it was also concluded that maternal body condition did not affect foetal sex ratio in buffalo. Our analyses failed to support hypotheses predicting that mothers will skew the sex ratios of their offspring in relation to their body condition. In this study, buffalo and elephant produced offspring with a sex ratio close to parity. Our results are discussed in light of the implications for testing such hypotheses in analyses of population level.

Key words: buffalo, elephant, local resource competition, Trivers–Willard hypothesis, sex ratios, *Syncerus caffer*, *Loxodonta africana*

INTRODUCTION

Hypotheses relating fitness to skewed sex ratios have been developed for various organisms and types of social organization. Most notable is the Trivers–Willard hypothesis (Trivers & Willard, 1973). Trivers & Willard (1973) suggested that females of polygynous species could increase their fitness by skewing the sex ratio of their offspring. The benefit of a skewed sex ratio would occur when a female could maximize her fitness through her offspring, in accordance with her present condition and the external constraints of the environment. Mothers in good condition, therefore, are expected to produce sons while those in poorer condition are expected to produce daughters (Trivers & Willard, 1973). The Trivers–Willard hypothesis is based on three assumptions. First, that the condition of the offspring will be correlated with that of the mother following the period of parental investment, second that the condition of the offspring will endure into adulthood, and third that male offspring will benefit differentially in reproductive success by slight increases in condition. Maternal lifetime reproductive success may not benefit most through the production of males. The advantaged daughter hypothesis suggests that mothers who are able to pass on rank or other such resources may gain the most reproductive benefit

through the production of daughters (Hiraiwa-Hasegawa, 1993; reviewed in Hewison & Gaillard, 1999). The advantaged daughter hypothesis has similar assumptions to the Trivers–Willard hypothesis (Hiraiwa-Hasegawa, 1993; Hewison & Gaillard, 1999).

As an alternative explanation for skewed sex ratios, Clark (1978) formulated the local resource competition hypothesis, which predicts that at the population level, mothers constrained by environmental conditions benefit by reducing resource competition through a skewed sex ratio biased towards the principal dispersing sex (Clark, 1978; Silk, 1983; Caley & Nudds, 1987). In African buffalo *Syncerus caffer* and savanna elephant *Loxodonta africana*, the sex that tends to leave the mother's social unit is the male, suggesting that in times of low primary productivity (characterized by droughts) and relatively high densities of animals, mothers would be best served by biasing the sex ratio of their offspring in favour of males.

The residual reproductive value hypothesis (Clutton-Brock, 1984; Cameron *et al.*, 2000) predicts that as mothers age, their reproductive effort will increase owing to decreasing conflict with current offspring. Very old mothers should, if this hypothesis holds for our study species, gain by investing in male offspring as these hold the highest potential fitness pay-off. Maternal age may also be related to condition, or act as a surrogate for an individual's ability to invest, though this remains a contentious issue (Saltz, 2001; Hewison *et al.*, 2002; Saltz & Kotler, 2003).

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The African buffalo is the largest member of the family Bovidae inhabiting sub-Saharan Africa. It reaches its southern distribution limit in northern South Africa (Skinner & Smithers, 1990). Buffalo are highly gregarious and form large herds comprising mainly females and juvenile males. Adult males are either solitary or congregate into bachelor herds, but do move in and out of the breeding herds on a transient basis (Sinclair, 1977; Skinner & Smithers, 1990). Males undergo intrasexual competition to maximize their fitness through access to oestrous females. Dominance is determined through agonistic behaviour and individuals achieving a high ranking are known to have longer attendance periods with oestrous females (Sinclair, 1977). Thus, male buffalo profit from maternal investment as their relative size plays a key role in determining their rank in the social hierarchy of bulls (Sinclair, 1977). In a survey of suckling calves, Pienaar (1969) found that males weighed more than females, highlighting the additional energetic cost to mothers in rearing their sons. Buffalo are sexually dimorphic, the bulls (590 kg) being larger than cows (513 kg), and the operational sex ratio is skewed towards cows (Pienaar, 1969). Sinclair (1977) suggested that buffalo in the Serengeti were limited by forage availability and quality. In Kruger National Park, food limitation may result from either low rainfall or increased conspecific density and subsequent intraspecific competition.

The African savanna elephant is distributed through large areas of sub-Saharan Africa, and in many nature reserves within South Africa (Skinner & Smithers, 1990). Elephants form matrilineal family groups. At the onset of puberty, however, bulls leave the maternal herd and either join bachelor groups or remain solitary (Skinner & Smithers, 1990). Within matrilineal groups rank is often determined by age (Buss, Rasmussen & Smuts, 1976). Bulls will rejoin herds to copulate with oestrous females. Elephants exhibit extreme sexual dimorphism with males (5500–6000 kg) attaining a much larger size than females (3630–3960 kg) and males compete for access to females (Buss & Smith, 1966; Skinner & Smithers, 1990). As in buffalo, the operational sex ratio favours females (Laws, 1969).

To test hypotheses relating to the skewing of sex ratios in buffalo and elephant the effects of lactation, maternal age, density, rainfall, and year on sex ratios at birth were examined in both species. Our analyses are based on several assumptions. The first is that nursing a calf in the year of conception will reduce a cow's condition owing to the energetic costs of lactation. Such cows should produce a higher proportion of daughters than non-lactating females (Rutberg, 1986). Furthermore, it was assumed that the age of the mother would be related to condition, with older cows in poorer condition than younger cows (Saltz, 2001; Saltz & Kotler, 2003). An increase in maternal age, however, may also be associated with the increased production of sons, leading to a male-skewed sex ratio; this would be because of an increased social status in females in relation to their age or size (Rutberg, 1983; Cameron *et al.* 2000; Côté & Festa-Bianchet, 2001). The final assumption

we made was that rainfall affects food availability and in years of higher rainfall cows should be in better condition than low rainfall years. In savanna systems, such as our study area, there is a direct relationship between rainfall and plant productivity (Coe, Cumming & Phillipson, 1976; Fritz & Duncan, 1994).

METHODS

Data obtained on African buffalo and savanna elephant living in the Kruger National Park (KNP), situated in north-east South Africa and extending over an area of 19 485 km² were analysed. The buffalo and elephant are counted annually during total aerial censuses of large mammals living in the park (van Aarde, Whyte & Pimm, 1999). From 1969 onwards, for some 30 years, culling has been used as a management tool to ensure that populations of both species remain within the limits proposed in the KNP masterplan (Joubert, 1986).

The age of culled buffalo was determined using dental wear patterns and the number of erupted incisors, based on published records for known-aged individuals (Grimsdell, 1973). Elephant age was determined using shoulder height and dentition (Sikes, 1967*a,b*; Hanks, 1972). Females were classified as lactating or non-lactating, based on the presence of milk that could be expressed from the teats. Buffalo calve throughout the year but have a definite increase in calving rates from January to April. Culls were conducted from May until December so a lactating cow was assumed to have a calf at foot. For elephants, lactation was assumed to indicate the presence of a pre-weaned suckling calf at the time of the cull. For both species, foetal sex was determined using characteristics of the external genitalia. A conception date was assigned to each foetus using a weight to age regression, based on Huggett & Widdas (1951) and Grimsdell (1973). For elephants, a revised regression was used to compensate for the length of gestation (see Craig, 1984). Our analysis of the influence of lactational status during conception on foetal sex was limited to multiparous cows. Based on annual censuses, three distinct population growth phases were identified in buffalo (pre-decline, decline and recovery) from 1984 to 1998. In elephant, two phases were noted (decline and recovery) from 1983 to 1996. As these periods may represent changes in local resource competition, foetal sex ratio was also investigated as a factor of these population growth phases, using year of conception as a variable.

To test whether local resource competition affected foetal sex ratios, each foetus was assigned a population density value for the year before conception from the region of its mother's herd. For management purposes, the KNP is divided into 4 regions (see van Aarde *et al.*, 1999) and the region of origin of each animal was included in our analyses.

To determine whether rainfall influenced foetal sex by influencing food availability/quality, each foetus was assigned a rainfall value based on the cumulative rainfall

recorded for a year before conception. Rainfall figures were available from 15 stations located throughout KNP. The rainfall value assigned to a foetus was the average of the weather stations in the management region from where it originated. The south region contained 5 stations, the central 4, the north 4 and the far north 2. For elephants that were culled before regions were differentiated for population surveys, the values for rainfall and density represent averages for the entire Park.

In 1998, additional information was collected for culled buffalo during a census primarily aimed at determining the prevalence of bovine tuberculosis in the KNP. Additional information consisted of a standardized index score of body condition that ranged from 0 to 5 (5 being the best condition), based on fat deposits along the back and rump region of the animal.

Foetal sex (male = 1, female = 0) was regressed against potential biologically meaningful interactions in a multivariate stepwise logistic regression (Hosmer & Lemeshow, 2000). The factors included were: (1) age (dummy variable for buffalo (all years) and continuous for elephant and buffalo (1998)); (2) KNP region (dummy variable); (3) rainfall; (4) density; (5) year of conception; (6) lactational status (dummy variable). All analyses were carried out in SYSTAT version 10 (SPSS Inc., 2000).

RESULTS

After investigating the correlation between possible factors influencing foetal sex ratios, both forward and backward stepwise logistic regressions were used on three sets of data yielding the same overall result. Three logistic models were developed: all buffalo foetuses (termed all years), only those buffalo foetuses recorded in 1998 when maternal condition was scored using a body condition index, and all the foetuses recorded for elephants.

The final model (Table 1) for buffalo over all years included only the constant term (which was not significant at $\alpha = 0.10$) and correctly predicted the foetal sex of both male and female foetuses 50.0% of the time (Table 2). A second model was developed specifically for buffalo culled in 1998, when an additional index of individual maternal body condition was recorded (Table 1). This model included maternal age and condition, both of which were significant predictors of foetal sex. However, while this model provided a better fit of the observed foetal sex ratio than the model that included all years, it only correctly predicted the foetal sex of both males and females 57% of the time (Table 2).

For elephants, the final model for foetal sex ratios included the region of KNP, the year of conception, and whether or not the mother was lactating at the time (Table 1). All variables were significant (at the $\alpha = 0.10$ level) compared to the reference category. For region, the southern region was used as a reference, while for lactational status the reference was lactating, with the exception of the far north region. Similar to the buffalo model, the elephant model correctly predicted the foetal

Table 1. Parameters for our backward stepwise logistic regression model for both buffalo *Syncerus caffer* and elephant *Loxodonta africana* foetal sex ratios in Kruger National Park, South Africa. The model follows the form:

$$y = \frac{\exp(\beta_0 + \beta_1(x_1) \cdot \beta_n(x_n))}{1 + \exp(\beta_0 + \beta_1(x_1) \cdot \beta_n(x_n))}$$

where β_0 is the constant and β_n the coefficient for the x_n parameter (ex. condition)

Model	Parameter	Estimate	SE	P-value
Buffalo (all years)	Constant	0.034	0.039	0.391
Buffalo (1998)	Constant	5.272	1.548	0.001
	Condition	-1.058	0.399	0.008
	Age	-0.191	0.067	0.005
Elephant	Constant	122.615	56.482	0.030
	Region ^a (A)	-1.042	0.492	0.034
	Region (C)	-0.631	0.281	0.025
	Region (FN)	-0.307	0.265	0.247
	Region (N)	-0.490	0.275	0.075
	Year	-0.061	0.028	0.030
	Lactating ^b (N)	-0.302	0.181	0.095

^a Reference region is the south; A, total park; C, central; FN, far north; N, north.

^b Reference category for lactational status is lactating; N, not lactating.

Table 2. Logistic model fit based on successful classification of foetal sex for both buffalo *Syncerus caffer* and elephant *Loxodonta africana* in Kruger National Park, South Africa

Model	Foetal sex	Observed	Model predictions		Predicted correctly
			Males	Females	
Buffalo (all years)	Males	1325	678.684	656.316	0.508
	Females	1291	656.316	634.684	0.492
	Total	2626			0.500
Buffalo (1998)	Males	66	41.696	24.304	0.632
	Females	48	24.304	23.696	0.494
	Total	114			0.574
Elephant	Males	308	156.875	151.125	0.509
	Females	306	151.125	154.875	0.506
	Total	614			0.508

sex of both male and female foetuses 51% of the time (Table 2). The implication of the low predictive ability of both buffalo and elephant models, suggests the equal probability of either a male or female foetus being observed is a binomial process.

DISCUSSION

The disparity between foetal sex ratios (essentially 1:1) and operational sex ratios for both species, which favours females, suggests either differential mortality among juveniles of each sex owing to differences in survival or the differential costs of maternal investment. Sinclair (1977) noted, however, that young buffalo predated by lions were taken in the same frequency as expected from their age

distributions after 1 year of age. Gestation among buffalo, and to a lesser extent elephant, occurs predominantly during the dry season when nutritional stress is highest for mothers. During this period the selective resorption of male foetuses, which may have increased energetic costs to mothers owing to their rate of growth, could also result in decreased male representation in the foetal sex ratio investigated (Rutberg, 1986). It has been suggested, however, that both sexes develop at the same rate during early embryonic development (Larson *et al.*, 2001).

While the variables included in the final models could function to skew sex ratios, the models themselves are unable to describe our observed sex ratio pattern. Supplemental data collected for buffalo in 1998, on individual measures of body condition, did not provide additional evidence for skewed sex ratios in this species. Indeed, the negative sign of the estimate for condition in our model suggests that good body condition is indicative of the increased probability of producing a female foetus. This is in contradiction to the predictions of the Trivers–Willard hypothesis. Our inability to successfully model foetal sex ratios in either buffalo or elephant may represent the result of two processes. First, environmental and maternal surrogates for individual condition are not highly correlated and second, these two species do not adjust their foetal sex ratio in relation to body condition.

Contrary to Rutberg's (1986) study on American bison *Bison bison*, African buffalo cows released from the energetic costs of lactation did not produce significantly more sons. Lactation was included in the elephant model and similarly to Rutberg's (1986) findings, cows that were lactating had a propensity to produce female offspring. Again though, the model failed to describe sufficiently the observed patterns of foetal sex ratios.

Females who fail to produce a calf in a given year and are, therefore, not lactating during the following year are not necessarily in better condition than those still lactating in response to their previous conception (Rutberg, 1986). Barrenness during a given year may result from heavy parasite load, chronic sickness, or social harassment, all of which would be reflected by a loss of condition. It was, however, not possible to measure these potential correlates of female condition. Linklater *et al.* (1999) found harassed female horses to be in poorer condition than non-harassed females. Cameron & Linklater (2000) also noted mares for which reproduction and maternal investment did not result in a loss of condition. Therefore, although as many correlates of condition as we had data available for were tested, it may be that other factors affected the observed foetal sex ratios.

Should age have an impact upon condition (discussed by Saltz, 2001; Hewison *et al.*, 2002; Saltz & Kotler, 2003), theory predicts that females in prime condition would preferentially conceive males (Trivers & Willard, 1973; Côté & Festa-Bianchet, 2001). Given this expectation, we would predict the production of an increased proportion of males with increased age. This may be owing to acquired experience, or the result of older individuals moving up the social hierarchy, or an increased opportunity to invest, as predicted by the residual reproductive

value hypothesis (Clutton-Brock, 1984; Cameron *et al.*, 2000; Côté & Festa-Bianchet, 2001). Green & Rothstein (1991), however, found that the final calves of female bison were almost always female. Females at the end of their reproductive lives should attempt to increase their lifetime reproductive success through the production and investment in the sex that would provide the largest reproductive pay-off. This follows since future competition with their youngest offspring is lowest and mothers may not have to worry about maintaining condition for the next reproductive cycle (Clutton-Brock, 1984; Cameron *et al.*, 2000). Age was included as part of the buffalo model (all years), but the sign of the coefficient indicates that as maternal age increases the probability of observing a male foetus declines. This corroborates the idea that age has a negative impact on condition (Saltz & Kotler, 2003), while opposing the residual reproductive value hypothesis and hypotheses concerning increasing maternal competence with age (Clutton-Brock, 1984; Cameron *et al.*, 2000; Côté & Festa-Bianchet, 2001).

Some species with a matrilineal social structure exhibit a female-skewed sex ratio among high-ranking individuals (Lloyd & Rasa, 1989; Festa-Bianchet, 1996; Nevison, 1997). In other studies, however, females of high rank produce more males (Clutton-Brock, Albon & Guinness, 1984; Cassinello & Gomendio, 1996). African elephants form female family units led by a matriarch, often the oldest female (Buss *et al.*, 1976). In a matriarchal society, the greatest benefit to the matriarch may be to produce a daughter who may inherit her status, in accordance with the advantaged daughter hypothesis (Hiraiwa-Hasegawa, 1993; reviewed in Hewison & Gaillard, 1999). In elephant societies, older females who are presumably of higher rank may, therefore, be expected to display a skewed sex ratio. Again though, the foetal sex ratios observed in this study were not affected by maternal age, as this did not seem to be a significant variable in the elephant model.

Rainfall has been found, in a savanna ecosystem, to directly affect primary productivity (Coe *et al.*, 1976; Fritz & Duncan, 1994). While individually, females may benefit from increased condition owing to rainfall through food availability/quality therefore producing more males (Trivers & Willard, 1973), several studies have shown that increased forage results in the production of a sex ratio skewed towards females (Pederson & Harper, 1984; Hoefs & Nowlan, 1994; Kojola, 1997). Similarly, studies have shown that nutritionally stressed deer produced a male-skewed offspring (Verme, 1985; Kojola, 1997). In our study, rainfall was not found to be a predictor of foetal sex in either buffalo or elephant. The inability of rainfall to significantly influence foetal sex ratios for either buffalo or elephant, despite the direct effect of rainfall on condition (Caron, Cross & du Toit, 2003), indicates that female condition does not affect the foetal sex ratios of their offspring. Since most buffalo in the KNP conceive between January and April, which corresponds to the late portion of the wet season, they may not be responding at the time of conception to previous rainfall, but anticipating the flush of grass coinciding with the calving season 11 months later. This would ensure optimal

forage availability and quality during lactation, when energetic costs would be greatest.

The production of female offspring in red deer *Cervus elaphus* increases with increased population density (Kruuk *et al.*, 1999). The underlying mechanism is linked to the energetic demand of juvenile males that cannot be met by their mothers. Subsequently, the high mortality rate of juvenile males results in a female-biased sex ratio (Kruuk *et al.*, 1999). High density can increase local resource competition in the same way that reduced rainfall does, through food limitation (Sinclair, 1977). Density was not, however, considered in any of our models of foetal sex. In this study, densities may not have been high enough to elicit a response in foetal sex ratios due to competition, although the same densities have been found to have a negative influence on overall population growth in buffalo and elephant (van Aarde *et al.*, 1999; Ogutu & Owen-Smith, 2003). The trend in population numbers during the study suggests that varying levels of resources would be available to mothers during this time. In the buffalo model that considered all years, annual variations owing to year were significant. The predictive power of the model, however, was no different than a binomial process of equal probability (i.e. flipping a fair coin).

One problem with the dispersion theory is that a calf produced in a bad year will not disperse quickly enough to alleviate the competition it may have with its mother. In addition, the calf entails an energetic cost for some time owing to the length of lactation in buffalo and elephant. A female buffalo has an 11-month gestation followed by 15 months suckling, or until the next calf is born (Skinner & Smithers, 1990). In total, a calf may remain with its mother for 2 years. Elephants have a 22-month gestation followed by a suckling period of up to 2 years (Skinner & Smithers, 1990). In elephants, the young may not disperse until puberty (~10 yrs) and female calves may remain philopatric (Skinner & Smithers, 1990). It seems unlikely then that the local resource competition hypothesis will hold for these two species because of the length of offspring dependency.

For this reason, the competition accrued on a local level is not alleviated by the production of a dispersing male calf. Conversely, if densities increase to the point of causing competition, the individual mother's share of the remaining forage would decrease. Consequently, her condition should decrease, at which point she would best benefit by the production of daughters (Trivers & Willard, 1973). If the mothers that survived the population decline experience decreased competition for food, they could produce female offspring without risking an increase in local resource competition (Clark, 1978). However, if those same females have increased access to quality forage (owing to decreased density), it is possible that their condition would increase, and they would gain the most benefit from the production of male offspring (Trivers & Willard, 1973; Kruuk *et al.*, 1999). The quality of forage available to an individual mother is relative to the number of individuals competing with her for the forage, which is based on rainfall. However, many other factors play a role in individual maternal condition.

The confounding nature of adaptive sex ratios has resulted in many conflicting results (Clutton-Brock & Iason, 1986). The lack of support for the Trivers–Willard hypothesis, as well as other hypotheses of skewed sex ratios, may result from the differential effect the maternal and environmental correlates investigated in this study have on individuals as opposed to populations.

In conclusion, the KNP buffalo and elephant populations do not regulate their foetal sex ratios. Indeed, foetal sex ratios follow a binomial process, with an equal probability of producing a male or a female foetus. However, further investigation into individual body condition is required. Even so, our model, which included individual condition, did not increase the explanatory power of the logistic model sufficiently to predict foetal sex ratios in a reasonable fashion. The assumptions made in this study were that the population level indicators of condition influence all individuals equally. Individual females, however, act to maximize their fitness within the environment they experience.

Acknowledgements

The National Research Foundation, the Conservation Ecology Research Unit and the South African National Parks funded the project. We thank Mrs Colleen Wood and Mr Obert Mathebula who assisted in fieldwork and the maintenance of the data used in this study. We also thank the South African Weather Bureau and the South African National Parks for access to their data. The preparation of this paper benefited from the comments and suggestions of Elissa Cameron, Bill Bateman, Chris Jerde, Tim Jackson, Patrick Duncan and Mark Hewison.

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