Annual and seasonal rainfall may influence progeny sex ratio in the black rhinoceros

Elizabeth V. Berkeley[1*] & Wayne L. Linklater[1,2]

[1]*Centre for Biodiversity and Restoration Ecology, School of Biological Sciences, Victoria University of Wellington, P.O. Box 600, Wellington 6140, New Zealand*

[2]*Centre for African Conservation Ecology, Nelson Mandela Metropolitan University, Port Elizabeth, South Africa*

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Facultative sex allocation theories predict that animals will bias their offspring's sex in response to environmental cues. Biased sex ratios can be a problem when managing small populations in the wild or captivity. Using rainfall and calving records from Hluhluwe-iMfolozi Park in South Africa, we compared seasonal and annual rainfall with calving rates and sex of the calves. Between 1989–2004, 159 calves were sighted soon enough after birth to reliably attribute their conception to a particular season and year. Conceptions were strongly seasonal, with most (73.6%) occurring during rainy seasons and the remainder during dry seasons. Overall progeny sex ratio for the period 1989–2004 was 53.1% male. Mothers were more likely to be observed with male calves if they conceived during the wet season (57.3% male) than during the dry season (42.9% male) in accordance with the Trivers-Willard hypothesis. Similar numbers of conceptions that resulted in calves occurred during wet and dry years (52.2% of conceptions occurred during wet years). Mothers were more likely to raise male calves if they conceived during wet years (60.2% male) than during dry years (46.1% male). Removal of males from small populations might be particularly important after a sequence of wet years to facilitate greater population growth.

Key words: ungulate reproduction, Perissodactyla, *Diceros bicornis* var. *minor,* sex allocation.

INTRODUCTION

Sex allocation theory and empirical tests suggest that maternal energy balance around or soon after conception influences birth sex (Clout *et al.* 2002; Roche *et al.* 2006; Cameron & Linklater 2007). Many species demonstrate changes in the birth sex ratio of their offspring in response to variation in food availability in accordance with predictions of sex allocation theory (Trivers & Willard 1973; Silk 1983). Shifts in birth sex ratios have important implications for wildlife managers since they can limit population growth by reducing effective population size, especially in small and fragmented populations (Wedekind 2002). By better understanding the mechanisms and environmental cues that influence birth sex ratios, we can develop strategies for managing animals both in captivity and in small reserves.

Hluhluwe-iMfolozi Park (HiP), South Africa, has the largest endemic population of the black rhinoceros *Diceros bicornis* var. *minor* and one of the few original populations remaining in Africa. This population is of strategic importance as a source for the managed rhino metapopulation (Emslie & Brooks 1999). Black rhinos in HiP show large variation in adult sex ratios across the park, though it is not clear whether this is due to management (*i.e.* selected removal of individuals for translocation) or a variation between the sexes in habitat preference (Reid *et al.* 2007). In African savanna habitats like those in HiP, range condition and the resources available to rhinoceros are closely related to rainfall because the availability of water strongly constrains plant growth (Emslie & Adcock 1994; Fritz & Duncan 1994). Previously, it was observed that birth sex ratios were positively correlated with rainfall in a small introduced population of black rhinos (Hrabar & Du Toit 2005). Our aim, therefore, was to establish if progeny sex ratios in black rhinoceros responded positively to rainfall modifications of the environment as has been reported in other ungulate species (Kruuk *et al.* 1999a; Garroway & Broders 2007). We expect wetter years and the wet season to correspond with the conception of more male calves. To this end, we obtained permission to use Ezemvelo

*To whom correspondence should be addressed.
E-mail: beaux.berkeley@vuw.ac.nz

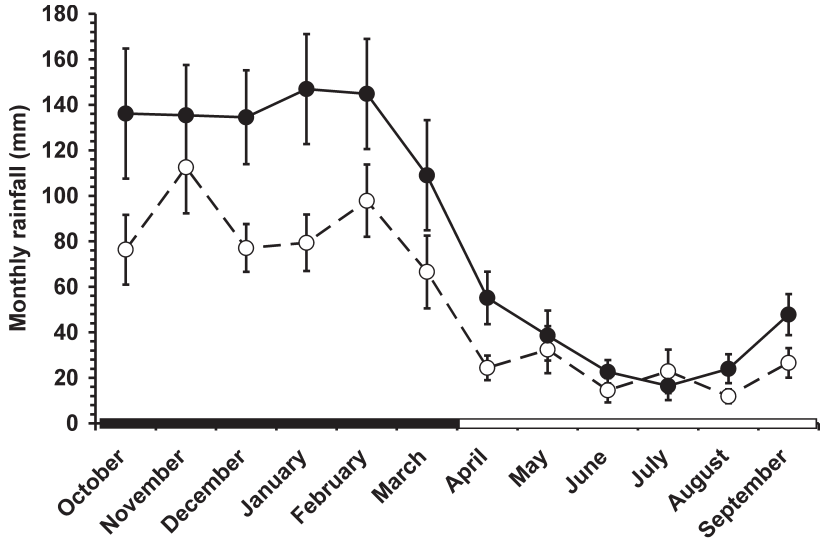

Fig. 1. Monthly rainfall (mm) from 1989 to 2004 at the northern (wet, ●) and southern (dry, ❍) rainfall stations of Hluhluwe-iMfolozi Park (Research Station and Makhamisa Station, respectively). The black portion of the horizontal axis indicates our classifications of the rainy season and the clear portion the dry season.

KZN Wildlife's long-term database on rainfall and black rhinoceros calf sightings by field ranger patrols in HiP to investigate the influence of seasonal and annual differences in range condition on conception rates and subsequent birth sex ratios.

METHODS

Data were collected in Hluhluwe-iMfolozi Park, which is approximately 90 000 ha in extent and located between S28.0000–28.43000 and E31.7160–32.0150 (Waldram *et al.* 2008). Annual rainfall is highly variable and seasonal, with wet, warm summers and cool, dry winters (Balfour & Howison 2002; Waldram *et al.* 2008). Monthly rainfall (mm) from 1989–2004 was characterized from records made at two weather stations that represent the Park's wetter north and drier south. Annual rainfall was averaged for the 14 years beginning with the onset of the rainy season in October. Years were classified as wet or dry if they were above or below the calculated average, respectively.

By the end of the study period (1989–2004), HiP had an estimated 235 black rhinos (Clinning *et al.* 2009). Records of calves sighted with marked mothers by field rangers and the calf's sex and size/age class when first sighted were used to place the calf's conception into a year and season based on the 15.3-month gestation of black rhinoceros. By using this subset of calves we have assumed that there is not a sex bias in the detectability of male and female calves after birth. Although black rhinoceros mothers are known to hide their calves during the first months *post-partum,* there is no evidence that one sex is better hidden than the other (Berger 1993). We compared conception rates and progeny sex ratios for calves conceived during wet and dry years and seasons. Progeny sex ratio results are reported as percentage male and Fisher's exact tests used for all comparisons.

RESULTS

Rainfall was strongly seasonal in Hluhluwe-iMfolozi Park (Fig. 1). Annual rainfall ranged from 465.7 to 1164.4 mm, and averaged 832.6 mm such that nine years were classified as wet years and six as dry years (Fig. 2).

Between 1989 and 2004, 159 calves were sighted soon enough after birth to reliably attribute their conception to a particular season and year. Overall progeny sex ratio for the period 1984–2004 was 53.1% male. Similar numbers of observed calves were conceived during wet and dry years (52.2% of conceptions occurred during wet years). Conceptions were, however, strongly seasonal, with most (73.6%) occurring during rainy seasons.

Mothers were more likely to be observed with male calves if they conceived during the wet season (57.3% male) than during the dry season (42.9% male) but the difference was only approaching significance (Fisher's exact test: $P = 0.077$, $n = 159$). Mothers were also more likely to raise

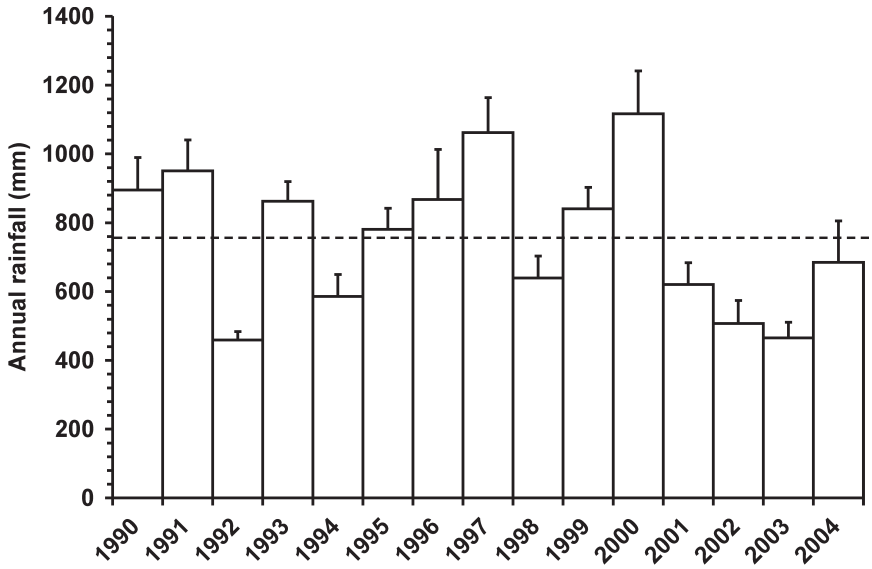

Fig. 2. Annual (October to September) variation in mean (±1 S.E.) rainfall from 1990 to 2004. The horizontal line indicates average annual rainfall over all years. Years with rainfall higher and lower than the average were classified as wet and dry years, respectively.

male calves if they conceived during wet years (60.2% male) than during dry years (46.1% male), although these results were also only approaching statistical significance (Fisher's exact test: P = 0.051, n = 159).

DISCUSSION

Evidence from HiP, one of the few large, wild and endemic populations of black rhinoceros, indicates that rainfall and, therefore, range conditions around conception influence seasonal conception rates and seasonal and annual progeny sex ratios. This result is similar to findings from other polygynous Perissodactyla (Monard *et al.* 1997). Higher birth rates were associated with conception periods during wetter seasons and corresponded with a statistically weak, but nonetheless relatively large, male bias in progeny sex ratios. Similar results were reported from black rhinos in the reintroduced population in Pilanesberg National Park (Hrabar & Du Toit 2005).

This study is limited to sightings of wild black rhinoceros calves whose exact birth dates are unknown. Progeny sex ratios, therefore, might be different from birth sex or even foetal sex ratios, since there may be sex-differentiated foetal and neonatal loss. The seasonal difference in progeny sex ratios might have been stronger if we had been able to observe birth or foetal sex ratios. In particular, it is known that male foetuses are vulnerable to poor maternal resources during mid- to late-gestation (Kruuk *et al.* 1999b; Linklater 2007 in rhinoceros; Stopher *et al.* 2008). Since the black rhino gestation is 15.3 months long, a calf conceived during the wet season is gestated through the dry season, whereas a calf conceived in the dry season is in late gestation during the wet season. Thus, for the larger number of conceptions during the wet season, there might be male-biased foetal loss that reduces an early post-conception male bias at parturition. Mid-gestation foetal loss during the wet season, however, is less likely to be male biased.

A better understanding of how range and climate conditions influence sex ratio dynamics may enable managers to identify appropriate rhinos from the source population for translocation. Reid *et al.* (2007) suggested that selecting specific animals for removal is important to maintain balanced social structures. After wet years, there may be a pulse of male recruitment so it may be advisable to schedule the removal of more males 4–5 years after a wet period when they become sexually mature and begin competing for mates. Heightened male–male competition for mates increases death rates and may impact female fitness (Linklater *et al.* 1999). Managers might remove old bulls that have already contributed progeny to provide space for the next generation or remove young males to contribute to new popu-

lations. Such a management strategy might be particularly important in small, confined populations where male–male conflict is the leading cause of death among males and young females reproducing for the first time (Brett 1998).

Our results provide support in the wild for the influence of maternal condition at conception on birth sex in black rhinoceros, as in several other large ungulates (Flint *et al.* 1997; Roche *et al.* 2006; Cameron & Linklater 2007), assuming that maternal condition for most prospective mothers correlates seasonally and annually with rainfall. In particular, our results support the contention that high birth sex ratios amongst captive black rhinoceros (Atkinson 1997; Dennis *et al.* 2007) might be lowered by reducing female body condition and restricting the diet of breeding mothers such that they are temporarily in neutral to negative energy balance for a period around and soon after conception.

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