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A captive population in crisis: Testing hypotheses for reproductive failure in captive-born southern white rhinoceros females

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ABSTRACT

The captive southern white rhinoceros (*Ceratotherium simum simum*) population is not self-sustaining. Many founders reproduced, but reproduction among captive-born (F_1) females has been extremely sluggish. Thus the conservation breeding program for this species faces a looming crisis. Using behavioral observations of a large captive population and a questionnaire survey circulated to facilities worldwide, several hypotheses for F_1 female reproductive failure were evaluated. Counter to predictions regarding behavioral deficiency in sociosexual behaviors, F_1 females were at least as proficient as F_0 females for all behavioral measures. Males also showed no sociosexual preferences for F_0 over F_1 females. Results indicate that most reproductive failure occurs post-copulation. The reigning root-cause hypothesis for F_1 female reproductive failure postulates that F_0 females are behaviorally dominant and suppress reproduction in F_1 females. However, no evidence for behavioral dominance was found and F_1 females housed with F_0 females were more likely to reproduce than those housed without F_0 females. Such social facilitation of reproduction is beneficial to F_1 female reproduction, but does not explain differential reproduction between F_1 and F_0 females. Because the design controlled for current conditions, these results point to development in captivity as the root cause of postcopulatory reproductive failure in F_1 females.

1. Introduction

Captive breeding is a significant component of conservation to the extent that self-sustaining populations can be maintained as a genetic reservoir should they be needed for reintroduction or population supplementation (IUCN, 1998). Captive release programs have met with mixed success (Wolf et al., 1998; Fischer and Lindenmayer, 2000), yet can play a significant role in recovery of individual species (e.g., Frantzen et al., 2001; O'Toole et al., 2002; Wanless et al., 2002; Britt et al., 2003; Green et al., 2005). The World Conservation Union (IUCN) recommends that captive breeding programs should be established before the in situ population becomes so precarious that removals will exacerbate its decline. However, many captive populations are not self-sustaining and some continue to rely on removals of animals from the wild. For captive populations in crisis behavioral research can play a critical role in identifying and solving problems with breeding

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and offspring survival (Kleiman, 1980; Lindburg and Fitch-Snyder, 1994; Wielebnowski, 1998; Swaisgood, 2004). Expression of appropriate social and reproductive behavior is one of the most common obstacles to conservation breeding, a problem that can be remedied by behavioral research (Lindburg and Fitch-Snyder, 1994; Wielebnowski, 1998; Swaisgood et al., 2000, 2003; Wanless et al., 2002; Fisher et al., 2003). Although informed changes in social management often successfully improve breeding success, few researchers have used a hypothesis-testing approach, which is necessary if the precise determinants of reproductive success and failure are to be understood.

We initiated a research program to address a crisis in conservation breeding for the southern white rhinoceros (*Ceratotherium simum simum*). White rhinoceros, formerly endangered, are now listed as conservation-dependent by the IUCN. More white rhinos have been exported from the wild than reside in captivity; thus captive breeding programs are failing. Global captive white rhino annual growth rate is projected at negative 3.5%, whereas growth rates in wild populations are 6–10% (Emslie and Brooks, 1999). The IUCN still supports captive breeding of white rhino as a safety net in case the political and social instability in the range countries reverses current population trends, as dramatically illustrated in other species such as black (*Diceros bicornis*) and Northern white (*Ceratotherium simum cottoni*) rhino (Emslie and Brooks, 1999). Many of the founding captive population of southern white rhino, given appropriate husbandry and management, reproduced well. Crucial to that success was the housing of rhinos in larger enclosures containing at least one male and several females (Rawlings, 1979; Lindemann, 1982; Fouraker and Wagener, 1996), an environment that would be more consistent with conditions in the wild, where males have access to several females and breed polygynously (Owen-Smith, 1975). However, reproduction among captive-born (F_1) females has been extremely sluggish (Emslie and Brooks, 1999; AZA, 2004), with as few as 8% reproducing in some populations (Schwartzenberger et al., 1999). Because males continued to sire offspring with wild-caught (F_0) females, the problem lies with the F_1 females. This situation is destined to deteriorate further as the F_0 females that formerly drove population growth begin to die off. Thus there is an urgent need to solve this conservation breeding problem soon or face the dilemma of further captures of wild rhinos to support the captive population.

Significant headway has been made in trying to determine what factors cause reproductive failure in F_1 females. For example, a number of investigations have detailed the pattern of reproductive hormones across the reproductive cycle (Schwartzenberger et al., 1998; Patton et al., 1999; Brown et al., 2001; Carlstead and Brown, 2005). Although anomalies in the reproductive cycle have been found, they are no more common in captive-born than wild-caught females, and so do not explain why more captive-born females fail to reproduce (Schwartzenberger et al., 1998; Patton et al., 1999). Endocrine data also indicate that age does not affect cyclicity (Brown et al., 2001). Why do white rhino females breed well when brought into captivity from the wild, but produce F_1 female offspring that fail to reproduce? There are plenty of examples of reproductive problems in conservation breeding programs, but we are not aware of any where the primary problem is limited to the F_1 generation. The case of the white rhinoceros is one of the great unsolved mysteries of animal reproduction in zoological institutions, a problem which has remained intractable despite considerable previous scientific effort.

Several hypotheses have been advanced to explain reproductive failure in F_1 females. Some of the hypotheses are specific to the immediate causal mechanism (e.g., abnormal endocrine cycles discussed above), while others postulate root causes. By far the root-cause hypothesis most strongly advocated by rhino managers and scientists is reproductive suppression of F_1 females by the older F_0 females sharing the enclosure (Anonymous, 2001; Carlstead and Brown, 2005); however, there are no data to support this contention. Reproductive suppression, in which dominant individuals suppress reproduction in subordinates at behavioral and/or physiological levels, has been observed in several mammalian species. These species, however, tend to be highly social with well developed dominance relationships (Abbott, 1987; Faulkes et al., 1990; Creel et al., 1992; Solomon and French, 1996; Creel et al., 1997), a social system quite divergent from the relatively fluid social system of white rhinoceros in nature (Swaisgood, unpublished data, Owen-Smith, 1975). Moreover, these field studies revealed no evidence of reproductive suppression or dominance. Nonetheless, the prevalence of reproductive failure among F_1 females raises the possibility that captivity may somehow promote stress and reproductive suppression, perhaps as a result of social density (reviews in: Hofer and East, 1998; Wielebnowski, 1998; Morgan and Tromborg, in press). Indeed the cheetah (*Acinonyx jubatus*) does not possess a social system typically seen in species with reproductive suppression, yet ovarian cyclicity is suppressed by the presence of female conspecifics in captivity (Wielebnowski et al., 2002).

Here we test several predictions of the reproductive suppression hypothesis in white rhinoceros. We also attempt to pinpoint where in the chain of events necessary for successful reproduction the breakdown takes place, by comparing several measures of reproductive proficiency in F_1 and F_0 females.

2. Methods

2.1. Observational study

Behavioral observations were made on 6 F_0 adult females (wild-born) and 5 F_1 (captive-born) adult southern white rhinoceros females residing in a 90-acre enclosure at the San Diego Zoo's Wild Animal Park (SDZWAP). For details see Patton et al. (1999). There was only one adult male present at a time, but males were exchanged midway through the study (both were wild-born). There were between 2 and 4 subadults present. Adults were females >5 years of age or females displaying regular reproductive endocrine cycles (Patton et al., 1999). Group composition changed during the 4-year study, consisting of 11–14 individuals at any given time.

Daily observations were made during active periods (unpublished data), the first and last 3 h of daylight. A total of 3827 h of data was collected using 1-h focal-animal