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Research paper

Bull access influences fecal progesterone metabolites in managed female white rhinoceros (*Ceratotherium simum*): Insights from hormonal and behavioral monitoring at The Wilds

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ABSTRACT

Refined husbandry has greatly improved reproduction in managed white rhinoceros, yet consistent breeding success remains a challenge. Social factors, particularly lack of mature bull access, are suggested contributors to reproductive challenges but supportive data is limited. At The Wilds, a large-landscape conservation center in Cumberland, Ohio, four postpartum multiparous and one nulliparous female white rhinoceros were monitored over a 10-month period. Fecal progesterone metabolite (fPM) assays and behavioral observations were conducted across three sequential conditions: indoor housing without a mature bull, pasture without a mature bull, and pasture with a mature bull. Baseline fPM values averaged 30 ± 1 ng/g in the postpartum, multiparous animals and 33 ± 3 ng/g in a nulliparous female. These values remained stable until a novel, mature bull was introduced, after which increases in fPM ranging from 131 to 174 ng/g, indicative of reproductive activity, were observed in four females following receptivity to mounting and copulation. A single smaller increase of 57 ng/g was recorded in the remaining female with limited reproductive behavior. Fecal testosterone metabolite analysis demonstrated that concentrations in the mature bull were significantly higher than those measured in the young males (≤3 years old) present throughout all conditions, thereby confirming the juvenile status of the latter. The results of this study suggest that the introduction of a mature bull can stimulate reproductive activity in female white rhinoceros following a prolonged period of quiescence.

1. Introduction

Maintaining viable populations in managed care may facilitate the conservation of many wildlife species. Yet in ex-situ programs, conservation efforts face ongoing hurdles, including health conditions unique to managed care and persistent reproductive challenges [1–3]. Rhinoceros are no exception as zoo-managed animals contend with prevalent diseases and reproductive obstacles, including unsuccessful breeding events and reproductive pathologies (e.g., uterine leiomyoma) [4–7].

Historically, among the rhinoceros taxa in ex-situ care, white rhinoceros (*Ceratotherium simum*) reproduction has been consistently lower than that of black rhinoceros (*Diceros bicornis*) and greater one-horned rhinoceros (*Rhinoceros unicornis*) [8,9]. Past investigations into factors potentially contributing to white rhinoceros breeding outcomes identified dietary imbalances, environmental conditions, and social dynamics [10–14]. Fortunately, more recent management efforts have resulted in improved white rhinoceros reproductive performance [3]. Female white rhinoceros once considered reproductively inactive or "flatliners" have resumed estrus and calved and reproductive success in North American females over ten years old now reaches 62% (J. Capiro, personal communication), a 20% increase over historic averages [3,15]. Included in these statistics however are some female rhinoceros that produce a single calf but fail to breed again for years, if at all. Given these ongoing challenges, it is important to continue investigating factors possibly associated with white rhinoceros reproductive dysfunction.

Potential social influences on female reproduction are complex and often inferred from keepers' observations and a few previous studies [6,13,14]. As a social species, much like elephants, white rhinoceros appear to benefit from certain group composition conditions such as access to

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conspecific females and the introduction of unfamiliar bulls [14,16–18]. A previous study reported endocrine changes in some females following the introduction of new males [6]; however, prior male exposure and the extent of physical access were not consistently defined. The management strategy employed by The Wilds, a large-landscape conservation center, offered the opportunity to focus specifically on the impact of the bull's absence and presence in shared space with females. Therefore, the objective of this study was to conduct a direct comparison of fecal progesterone patterns, accompanied by reproductive behaviors, in female white rhinoceros with and without prolonged physical access to a mature bull.

2. Materials and methods

2.1. Housing

The management structure at The Wilds in Cumberland, Ohio provided a unique opportunity to examine the influence of mature bull access on female reproductive activity. From November 2023 through April 2024, females and juvenile males ($\leq$3 yrs old) were housed as a bachelorette crash in Barn A, whereas the proven mature bull was housed separately in Barn B (Fig. 1). The two barns were 180 m apart and did allow for potential olfactory access but eliminated visual and physical access. On warmer days (>10°C) throughout this time, the bachelorette crash was allowed outdoor access into the pens attached to Barn A. However, due to a medical issue, the mature bull was not allowed outdoor access until after the bachelorette crash had been moved to pasture. On April 3, 2024, the bachelorette crash was moved to pasture, and the mature bull joined five months later on September 1, 2024. All animals remained together until the end of the study (October 31, 2024) and only returned to indoor housing when cooler temperatures arrived (November 20, 2024).

To facilitate interpretation, housing and physical access to a mature bull were categorized into three distinct conditions. Condition 1 (C1: 121 d) represented the time the bachelorette crash was indoors without a mature bull. For condition 2 (C2: 152 d), the bachelorette crash was on pasture without a mature male, whereas during condition 3 (C3: 60 d), all rhinoceros including the mature bull shared a pasture.

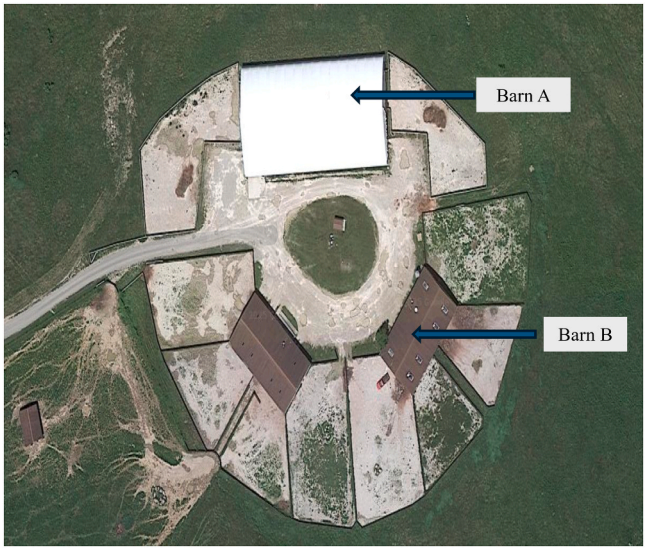


Fig. 1. Fall and winter housing for rhinoceros at The Wilds in Cumberland, Ohio. During the cool weather months, female and juvenile male white rhinoceros (*Ceratotherium simum*) were moved into Barn A, whereas the mature male was housed in Barn B.

2.2. Animals

The initial study cohort was comprised of four multiparous females (Females 1–4) at different postpartum stages (Table 1), each accompanied by a nursing calf. During C2, a nulliparous female (Female 5) was added after a juvenile male displayed reproductive behaviors towards her. Behavioral observations and fecal sampling were extended to the mature bull (Male 1) and two young males (Male 2 and Male 3) through C2 and C3. Male 1, a proven male that had previously sired 15 calves at two institutions, arrived at The Wilds in October 2022. Until C3 of this study, Male 1 was only housed in Barn B and had not been introduced to any of the females at The Wilds. Male 2 was a juvenile male just over three years old by the end of the study, and Male 3 was the nursing calf of Female 3 and just over two years old by the study's end.

2.3. Behavioral observations

In addition to hormone monitoring, reproductive behaviors were recorded in C2 and C3 using a published ethogram (Table 2). The aim of these observations was to provide behavioral corroboration for fPM trends in relation to the presence or absence of reproductive activity. Because an intern was not available until late in C1 and reproductive behaviors were not anticipated from the indoor-housed crash, observations were limited to C2 and C3. The trained intern conducted whole group observations from a pickup truck parked to allow a near-full view of the pasture and moved as needed when a low crest disrupted visibility.

A ten-minute acclimation period preceded each session, during which the intern confirmed the identity and location of all study animals. If one or more animals could not be seen from a single location, the intern would reposition at 15-minute intervals to obtain visibility, and a five-minute acclimation period followed each move. Although longer acclimation periods are more typical in other studies, the herd at The Wilds is routinely exposed to vehicles ($\geq$1 vehicle per hour) from tours and staff. Per The Wilds staff, the intern's movements were not expected to disturb normal activity.

In C2, observations were conducted for 45 min between 09:00 and 12:00 once daily, five days a week. In C3, observations were performed twice daily, five days a week, and for 90 min: between 09:00 and 12:00 and 15:00 and 17:00. The changes in protocol were due to the anticipated increase in behaviors upon the introduction of the mature bull. During each session, all reproductive behaviors and relevant context were recorded, including behavior initiation and recipient, length of

Table 1
Demographic characteristics of male and female white rhinoceros (*Ceratotherium simum*) included in this study. Post-partum represents the number of months since calving by the end of the study. Pregnancy status was determined by serum progesterone values 6 months after the end of the study and successful parturition 16 months after the end of the study.

Animal	Sex	Age (years)	Parity (Number of prior births)	Sex of nursing calf	Post-Partum (month)	Pregnancy status
Female 1	F	11	Multiparous (3)	Male	10	Pregnant
Female 2	F	15	Multiparous (5)	Female	13	Not pregnant
Female 3	F	10	Multiparous (2)	Male	23	Pregnant
Female 4	F	13	Multiparous (2)	Female	8	Not pregnant
Female 5	F	5	–		NA	Not pregnant
Male 1	M	33	–		–	–
Male 2	M	3	–		–	–
Male 3*	M	2	–		–	–

*Nursing calf of Female 3.

Table 2
Reproductive behaviors recorded for female white rhinoceros (*Ceratotherium simum)*. A trained observer conducted 45-minute sessions when the females were housed without the mature bull and 90-minute sessions after the bull was introduced, noting each listed behavior shown by or directed toward the females.

Behavior	Description
Chin Rest	Chin placed on another individual, only indicated adult pairing.
Copulation	Penetration of penis into vagina.
Mount	Bull placed forelegs on cow's back and attempts penetration. May not be solely sternal to dorsal (e.g., bull attempts to mount from side).
Hic/Vocalization	Repetitive, throbbing inhalation; wheezy exhalation.
Vulvar Wink	Rapid contraction of vulva; might include lots of urine squirting.
Vulva Swelling	Swelling and/or dilation of vulva.
Vaginal Discharge	Thick mucus discharge around vulva.
Urine Squirting	Typically short bursts of urination from female. Typically in combination with a tail lift and vulvar winking in females.
Tail Raise	Female's tail is raised and curled away from genitals. Typically in combination with urine squirting and vaginal winking.
Follow/Approach	Intentional following/approach of female by bull or vice versa.
Anogenital Investigation	Bull smells female's vaginal area; often followed by flehmen.
Penis unsheathed	Penis dropped from the sheath, possibly in a partial erection.

time of action, and whether the behavior was accepted or rejected. For example, we noted if a female stood or moved away during mounting attempts. Although all juvenile and adults (n = 11) were monitored continuously, focal attention was given to study individuals. At the termination of each session, the intern would drive within 30 m of individuals and use binoculars to look for any indications of vaginal discharge or swelling. The Wilds staff would also inform the intern of any breeding events observed during the study and outside of behavioral sessions.

2.4. Fecal collections and assay

All fecal samples were collected with approval from the Cincinnati Zoo & Botanical Garden's IACUC under IACUC protocol 22–175. Fecal sampling began in November 2023 for the two females that had already calved (Females 1 and 3), whereas collections from the remaining parous females (Females 2 and 4) began once they were separated for calving in December 2023 and February 2024, respectively. Fecal samples were collected from the remaining rhinoceros (Female 5 and Males 1–3) after May 1st, 2024. Collections included one to three weekly samples until October 31, 2024. To ensure fecals were obtained from known rhinos, the trained intern collected freshly defecated samples before they became contaminated by others in the crash. During C1, the intern collected the samples when the crash was moved to a separate area of the barn for cleaning. During C2 and C3, the intern would drive a pickup to the midden as soon as the identified rhinoceros had finished defecating to collect the fresh sample.

In preparation for enzyme immunoassay (EIA), 0.5 g of fecal material were extracted in 5 mL of 90% ethanol and agitated for $\geq$ 12 hr on a mechanical rocker. Samples were then centrifuged at 2900x*g* for 15 min before resulting supernatant was pipetted into cryovials for storage at −20°C until analysis. Using previously validated antibodies, fecal progesterone metabolites (fPM) and fecal testosterone metabolites (fTM) were quantified with progesterone and testosterone mini-kits (ISWE003, ISWE001, Arbor Assays, Ann Arbor, MI) [19–21]. Current kit insert instructions were followed except volumes of sample, antibody, and conjugate were modified to 50, 25, and 25 µl, respectively. All samples and standards were analyzed in duplicate.

2.5. Determination of reproductive activity

Baseline fPM concentrations were established for each female using an iterative exclusion process. From each full dataset, the mean (μ_o) and standard deviation (SD) were calculated before removal of any values exceeding μ_o + SD. The dataset was reset and the process repeated until no values remained above the μ_o + SD threshold. The final stabilized μ_o was set as the baseline (BL) and used to establish an additional threshold of 2BL. Reproductive activity was defined as at least three fPM values exceeding 2BL within a 14-d period [8,22]. Profiles that failed to meet reproductive activity requirements were labeled as static low (i.e., fPM fluctuations <2BL).

2.6. Statistical analyses

All statistical analyses were conducted in R 4.4.2. To determine if condition influenced the likelihood of reproductive activity occurrence, fPM data from each rhinoceros were pooled by condition and analyzed with a generalized mixed model (GLMM). Contrasts among the three conditions were evaluated with a Bonferroni-adjusted post-hoc test. Presence of reproductive activity served as the binary response, condition as the fixed effect and individual as the random intercept. Due to the lack of observed behaviors in C2, statistical analysis of behaviors in relation to condition was not possible. Instead, the time between repeated ($\geq$2 behaviors/session) behaviors such as tail raising and urine squirting, along with mounting and copulation events, were noted in association with peak fPM values. To compare fTM concentrations among the three males, a Kruskal-Wallis followed by a Dunn's pairwise were performed.

3. Results

3.1. Female fPM and behavior

C1 - The fPM concentrations of all four multiparous female rhinoceros remained below the reproductive activity threshold through C1 (Fig. 2) with an overall mean of 34 ± 1.8 ng/g. A single point from Female 3 rose above 3 SD from baseline, but this increase was limited to the single datapoint. Therefore, C1 fPM profiles for all four females were defined as static low. Reproductive behavioral observations were not performed.

C2 – The overall mean fPM decreased to 29 ± 0.8 ng/g, and fPM concentrations in all female rhinoceros remained static low. Progesterone concentrations in Females 1 and 4 rose above 2BL briefly in two samples then quickly returned to baseline. No reproductive behaviors were displayed by any female rhinoceros. A juvenile male (Male 2) was observed exhibiting reproductive behaviors towards Female 5 (e.g., unsheathed penis, mounting attempts). Female 5 did not exhibit receptivity, moving away or failing to stand during these attempts. Consistent with these observations, the mixed-effects model indicated that C2 did not influence the odds of reproductive activity compared to C1 (P=0.73).

C3 – In C3, fPM concentrations of all five females rose above 2BL within 45 d of the introduction to Male 1 and remained elevated in at least three samples during a 14-d period, meeting the criteria for reproductive activity. Mean fPM in C3 increased to 43 ± 4 ng/g and reproductive behavior was observed in all rhinoceros in varying magnitudes (Figure S1). Peak fPM values were approximately threefold to fourfold above baseline in Females 1–3 and 5, and twofold in Female 4. In addition to the observed hormonal reproductive activity in Females 1–3 and 5, reproductive behaviors including repeated tail raising, urine squirting, and receptivity to mounting and copulation were observed before or after intervals of elevated fPM (Fig. 2; S1). In Female 4, reproductive behaviors were limited to two repeated occurrences of urine squirting and tail raising prior to the peak in fPM. The generalized linear mixed model detected a significant condition effect ($P < 0.001$),

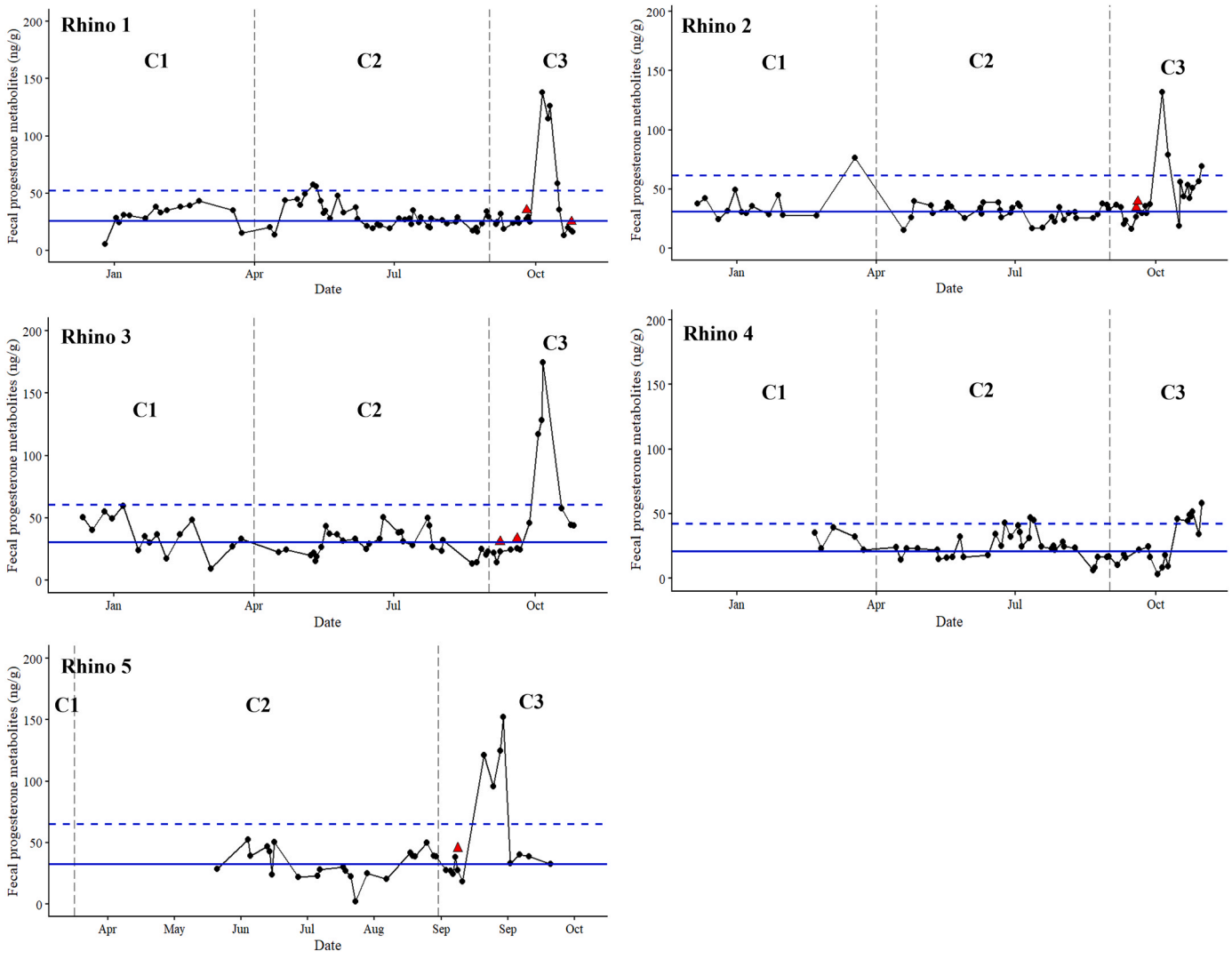


Fig. 2. Fecal progesterone metabolite (ng/g) profiles of female white rhinoceros ($N = 5$; *Ceratotherium simum*). Fecal collections were performed through three management conditions (C): 1) in the barn without mature bull access, 2) on pasture without mature bull access, and 3) on pasture with access to a mature bull. Horizontal lines demark individual rhinoceros baseline concentration (——) and baseline + 2 standard deviations (- - -). Approximate date of events of receptive mounting or copulation marked by triangles (▲).

signifying an increased likelihood of an fPM increase in C3 compared to C1 (P=0.011) and C2 (P=0.04).

3.2. Male testosterone

The mature bull's mean fTM increased by 31% from C2 to C3 (9.78 ng/g and 12.86. respectively). Mean fTM concentrations from the two younger males were similar across conditions. Mean fTM concentrations for Male 2 were 6.31 ng/g and 6.40 ng/g for C2 and C3, respectively. Similarly, mean fTM for Male 3 were 5.09 ng/g in C2 and 6.11 ng/g in C3. Across individuals, a Kruskal–Wallis test with Bonferroni-adjusted Dunn comparisons indicated the mature bull's mean fTM was significantly higher than those of both juveniles ($P < 0.001$), whereas the juveniles' mean fTM did not differ ($P = 0.373$; Fig. 3).

4. Discussion

This study provides strong evidence that direct access to a mature bull can play a significant role in female white rhinoceros reproductive activity, as defined by fPM patterns meeting the criteria consistent with ovarian activity. We expected some variation among the three conditions, yet fPM profiles remained static low until the mature bull's introduction, after which near synchronized increases in fPM occurred in all five females. Although the study was small, it provides solid scientific evidence that supports many past anecdotal claims and a recent study out of Europe [6] regarding the significant influence of a breeding bull on reproductive activity in white rhinoceros.

As managed white rhinoceros are not seasonal breeders, we did not anticipate a seasonality effect. Housing changes, particularly changes in outdoor access, have nonetheless altered reproductive activity in other non-seasonal species such as cattle and elephants [23–25]. In the present study, the transfer from indoors to outdoors may explain the slight rise in fPM values recorded for Females 1 and 4 during C2. These increases, however, observed 28 and 102 d after moving outdoors did not meet the criteria for reproductive activity (i.e., $\geq$3 values above 2BL). Increases in fPM also failed to recur and were not observed in the other three females, suggesting that the housing change did not substantially influence reproductive activity in this study.

Although we could not confirm ovulation in association with increases in fPM without ultrasonography, we believe ovulation likely occurred in Females 1–3 and 5 for the following reasons. Females 1 and 3 became pregnant, as confirmed by elevated serum progesterone concentrations 4–5 months after study conclusion and parturition

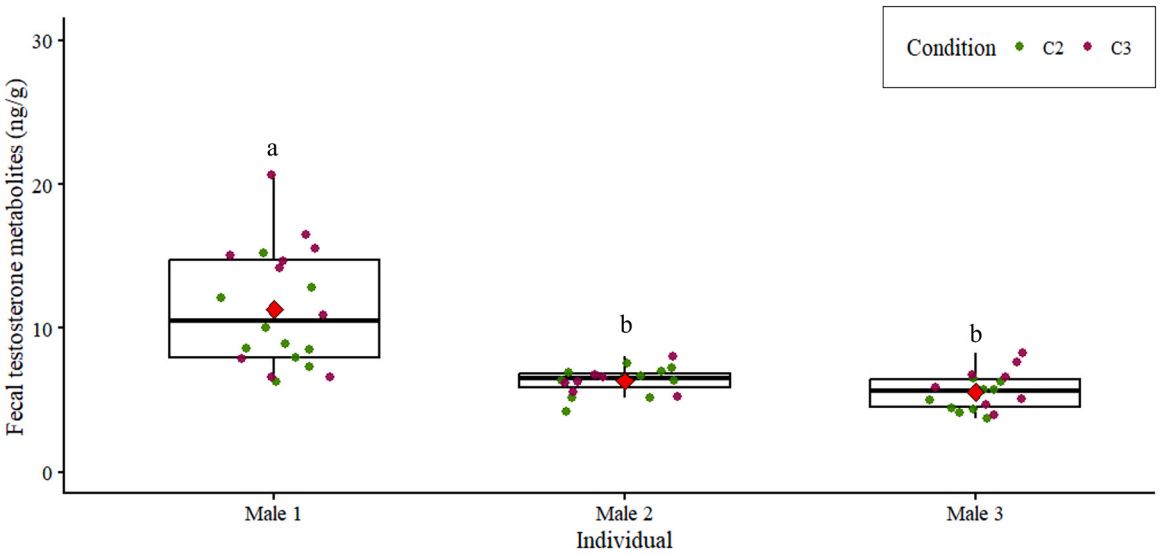


Fig. 3. Box-and-whisker plots of fecal testosterone metabolite (fTM) concentrations in male white rhinoceros (*Ceratotherium simum*). The mature bull (Male 1) was a proven breeder, 36 years old at the end of the study. Male 2 was three years old and Male 3 was two years old. Means are shown as diamonds (◊), and individual data points are colored by condition. Plots that do not share a letter differ significantly according to a Kruskal Wallis test followed by Dunn pair-wise comparisons, $P < 0.05$.

approximately 16 months later. A second breeding event was not observed in Female 3 after copulation in C3, but Female 1 did breed again following the mounting observed during C3. However, the timing of the second event, copulation 29 d after observed mounting, followed a luteal phase of normal ovulatory length. Females 2 and 5 did not conceive during C3, although each exhibited reproductive behaviors followed by an fPM rise to concentrations comparable to those of the females that did become pregnant in this study and to luteal phase profiles reported for other breeding females [26]. However, we do acknowledge that direct comparison of fPM concentrations with those reported in other studies is complicated by methodological differences, including differences in assay type (e.g., radio- versus enzyme-linked immunoassay and use of different immunoassay [27,28]. In contrast to the response of most study females, the C3 rise in fPM was less pronounced in Female 4, suggesting follicular luteinization rather than ovulation may have occurred.

Prior studies report a potential lactational anestrus of 8–13 months in white rhinoceros [18,29,30], which overlapped the postpartum timeline of Females 1, 2, and 4. Even so, increases in fPM and accompanying reproductive behaviors (i.e., mounting and copulation) occurred in Females 1 and 2 at or before the end of the presumed lactational anestrus period. The behavioral and hormonal patterns of Females 1 and 2 also aligned with those of the females that were not expected to experience lactational anestrus; Female 3, who was over two years postpartum and Female 5 who was nulliparous. Female 4 met the reproductive-activity criterion with a lower amplitude fPM increase and no clear reproductive behaviors, which may reflect lactational anestrus at eight months postpartum or simply individual variation. Review of the Zoological Information Management System (ZIMS) revealed substantial individual variation in postpartum conceptions, with some documented near three months postpartum and, in cases of calf loss, as early as 35 days [31,32]. Therefore, the static low fPM periods in C1 and 2 are likely at least partially due to the absence of a mature bull rather than lactational anestrus alone.

Throughout all conditions, juvenile males remained with the "bachelorette crash". Their presence introduced a potential confounding factor as females were not entirely without access to male rhinoceros. However, fTM concentrations in Male 2 and Male 3 were significantly lower than those in the mature bull (Male 1), indicating a male capable of breeding was not physically accessible until C3. Consistent with this fTM interpretation, female reproductive behaviors and fPM evidence of reproductive activity were confined to C3, indicating that juvenile male presence did not stimulate reproductive activity and direct access to a mature bull was needed. The mean fTM from Male 1 was 2.2 times the juvenile means, which falls within the reported 1.6–3.4 times increase for mature white rhinoceros bulls compared to males under five years of age [33].

It is important to note that the mature bull in this study was unfamiliar to the bachelorette crash. Early observations of bull-related stimuli likewise involved the introduction of a novel male [6,18]. Female mate choice has been suggested as a plausible explanation for these occurrences, as females that cohabitated for years with a familiar bull without conceiving resumed reproductive activity and conceived in some cases after introduction to a new male [6,34]. However, the presence of a novel bull did not trigger reproductive activity in all females since quiescence was documented in some females even following introduction to novel bulls, suggesting additional mate-choice criteria or other underlying physiological constraints [6, Metrione personal communication]. Future studies should examine whether periods of static fPM are similarly interrupted when access to a familiar bull is restored to distinguish the effects of male novelty from those of simple access.

5. Conclusion

The management system at The Wilds allowed for a study that examined the effect of direct mature bull access on female white rhinoceros reproductive activity. After prolonged periods of static low fPM in the absence of a mature bull, introduction of the novel breeding bull was associated with fPM increases indicative of reproductive activity in four of five females, concurrent reproductive behaviors, and two pregnancies. Juvenile males, present throughout, exhibited significantly lower fTM and did not elicit comparable female responses, indicating that direct access to a mature bull, and not juvenile male presence, is the salient stimulus. These findings can be translated directly to management recommendations that may further improve white rhino reproductive performance as females presumed reproductively inactive, hormonally or behaviorally, may simply require mature bull access for breeding to resume.

CRediT authorship contribution statement

Kandace Krupp: Writing – review & editing, Investigation. **Caitlin Consago:** Writing – review & editing, Investigation. **Terri L. Roth:** Writing – review & editing, Supervision, Methodology, Conceptualization. **Shauni Windle:** Writing – review & editing, Writing – original draft, Visualization, Supervision, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Dan Beetem:** Writing – review & editing, Supervision, Resources, Methodology, Investigation, Conceptualization. **Cody Cseplo:** Writing – review & editing, Supervision, Resources, Methodology, Investigation, Conceptualization. **Elizabeth Donelan:** Writing – review & editing, Supervision, Investigation, Data curation.

Declaration of Competing Interest

All authors of the submitted manuscript, "Bull access influences fecal progesterone metabolites in managed female white rhinoceros (*Ceratotherium simum*): Insights from hormonal and behavioral monitoring at The Wilds" declare no conflicts of interest.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.therwi.2026.100166.

Data availability statement

The data that support the findings of this study are available from the corresponding author upon reasonable request.

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