

DIFFERENTIAL INVESTMENT IN SONS AND DAUGHTERS: DO WHITE RHINOCEROS MOTHERS FAVOR SONS?

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In species in which one sex experiences greater variation in lifetime reproductive success than the other, the Trivers–Willard hypothesis predicts greater parental investment in offspring of the more variable sex. Support for this hypothesis has been inconsistent and few studies have determined whether differential allocation of resources can be attributed to the parent (as predicted by sex-biased parental investment) or to efforts by offspring to extract resources. We addressed this issue by characterizing maternal investment in wild white rhinoceros (*Ceratotherium simum*). In a 3-year study, we radiotracked 14 adult females and recorded behavioral activities related to both maternal investment and offspring extraction of maternal resources. Investment in sons appeared to be greater than in daughters: sons suckled significantly longer and more frequently and were weaned significantly later than daughters. Although mothers did not respond differentially to individual nursing solicitations from male versus female offspring, our results suggest that mothers invested more in sons that vocalized at higher rates, but did not alter their investment in daughters in response to call rate. This may indicate that mothers, in part, facilitate access to resources depending on the sex of their offspring. This study provides a useful model for determining whether sex-biased investment is under maternal control or is a consequence of sex differences in the offspring's efforts to extract parental resources.

Key words: *Ceratotherium simum*, maternal investment, rhinoceros, sex allocation, signaling

In species with multiple reproductive bouts, investment in current offspring detracts from the resources available to invest in future offspring. Consequently, when the fitness consequences of producing sons differ from those of producing daughters, natural selection should favor maternal ability to alter investment in male versus female offspring in response to resource availability (Frank 1990; Trivers and Willard 1973). For example, in polygynous species, male reproductive success can be highly variable, with high-quality males monopolizing breeding opportunities with females (Emlen and Oring 1977). If maternal condition influences the quality and, hence, the reproductive success of her offspring, then mothers in good condition are expected to invest more in sons, because their sons will have the highest probability of competing successfully for mates. In contrast, mothers in poor condition should invest more in daughters because a low-quality daughter will produce more offspring than a low-quality son. Mothers could

differentially allocate resources to offspring by manipulating the primary sex ratio (prenatal investment), or by altering maternal interactions that increase offspring quality postpartum (postnatal investment).

Although the Trivers–Willard hypothesis (TWH—Trivers and Willard 1973) is conceptually clear, it has proven difficult to test for a variety of reasons. Empirical tests of prenatal adjustments to the 50:50 sex ratio have figured more prominently than studies of postnatal sex-biased investment in offspring, but these tests suffer from a variety of shortcomings, including poor understanding of the underlying physiological mechanisms (Cameron 2004; Hewison and Gaillard 1999; Sheldon and West 2004). Postnatal tests of the TWH also have been complicated and have produced equivocal results. For example, tests of sex-biased resource allocation in species with sex-biased dispersal can be difficult to interpret because alternative hypotheses also predict differential investment in the dispersing sex (e.g., Cockburn et al. 2002). This problem is found in many mammalian species, where males are often the dispersing sex (Greenwood 1980; Pusey 1987), rendering interpretation of sex-biased investment difficult.

Another problem prevalent in tests of postnatal sex-biased investment is that, although the TWH assumes that the mothers

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adaptively manipulate resource distribution to their offspring, few investigators address this assumption. Although several studies provide evidence for differential extraction of resources by offspring, few studies have demonstrated that mothers alter resource allocation to their progeny (Brown 2001; Clutton-Brock 1991). Sex-biased extraction of resources, although often leading to the same outcome as that predicted by sex allocation theory, can be explained by the self-interested actions of the offspring. Simply demonstrating that one sex receives more resources than the other, while consistent with the TWH, is not a definitive test. One way of addressing this problem is to show that maternal response to offspring solicitations is stronger for one sex than the other. Thus, a potential solution to this conundrum can be found by investigating the interplay between offspring signals of need and maternal response. If mothers respond differentially to feeding solicitations from sons and daughters, then it can be inferred that mothers, in part, are adjusting their allocation of resources in favor of one sex.

The social and mating system of the white rhinoceros (*Ceratotherium simum simum*) makes these animals a good species for testing TWH predictions for sex-biased investment. Although several adult males are often present on a territory, only the dominant bull has reproductive access to females traversing his territory (Owen-Smith 1971, 1975). Male reproductive success is highly variable, with a dominant male producing more offspring than the average female, and the average female producing more offspring than a subordinate male (Owen-Smith 1988). Dominance relationships among females are poorly developed or nonexistent, and therefore play little or no role in female reproduction in either captive or wild settings (Swaigood et al. 2006). Dispersal patterns in white rhinoceros are largely unknown, although a few cases of female dispersal have been documented (Owen-Smith 1988). In our study population, where removals from designated areas are conducted every year, both males and females move into the newly unoccupied habitat, suggesting that both sexes may disperse.

We performed a longitudinal study on white rhinoceros to test the predictions of the TWH. Specifically, we predicted that mothers in good condition should bias investment toward sons compared to daughters. By examining patterns of maternal investment in relation to offspring sex, age, and signals of need, we provide the 1st quantitative data on the mother–infant relationship in this species and evaluate whether sex-biased investment is due to greater allocation of resources by the mother or greater extraction of resources by the offspring.

MATERIALS AND METHODS

Study area and population.—This study was conducted in the iMfolozi section of Hluhluwe–iMfolozi Game Park, KwaZulu/Natal, South Africa (28°S, 31°E). iMfolozi is characterized predominantly as savanna–bushveld habitat. Average annual rainfall is 650 mm with the majority of rain falling in the summer months between October and March. Consequently, there is a distinct wet and dry season in the area. Annual temperatures range from 13°C to 35°C. Historically, iMfolozi is

known for having saved the white rhinoceros from extinction, harboring the last remaining population at the turn of the 20th century. Annual aerial counts estimate that more than 1,600 white rhinoceros are located in 965 km². Population growth rates are estimated at 7% and white rhinoceros are removed annually from iMfolozi to offset population growth and to restock other reserves (Owen-Smith 1981). iMfolozi contains several ungulate species including black rhinoceros (*Diceros bicornis minor*), African bush elephant (*Loxodonta africana*), giraffe (*Giraffa camelopardalis*), African buffalo (*Syncerus caffer*), and blue wildebeest (*Connochaetes taurinus*); as well as a suite of predators including lion (*Panthera leo*), spotted hyena (*Crocuta crocuta*), leopard (*Panthera pardus*), cheetah (*Acinonyx jubatus*) and African wild dog (*Lycan pictus*).

Data collection.—We placed Telonics radiotransmitters (Telonics, Inc., Mesa, Arizona) in the horns of 14 adult females (for protocol see Shrader and Beauchamp 2001). Females were followed circa weekly throughout the battery life of their transmitters (approximately 2 years) and 4 females were refitted with new transmitters when their old transmitter battery died. Twelve of the 14 females monitored were accompanied by a dependent calf at the time of radiotransmitter placement. The 2 females without calves were assumed to be nulliparous based on estimates of their age, but gave birth later in the study (one producing a son and the other a daughter). Although the parity of the females with dependent calves was unknown, age estimates based on horn development suggest that they were multiparous. Seven of these females weaned existing calves and gave birth to another during the study. All females were in notably good condition throughout the duration of the study (based on body condition criteria established by Reuter and Adcock [1998]). The white rhinoceros population at iMfolozi is growing rapidly, but managed below carrying capacity by frequent removals for translocation to other reserves (Owen-Smith 1981). The habitat in the reserve is highly suitable for this species (Owen-Smith 1973). Thus, for females in good condition living in an environment with ample resources, the TWH predicts male-biased maternal investment.

Calves were placed into 4 age classes based on developmental phases. From birth to 6 months of age (class A), calves are almost exclusively dependent on their mother for their nutritional requirements. Between 6 and 12 months of age, calves' nutritional requirements are met through a combination of nursing and grazing (class B). At 12 months of age (class C), calves graze as frequently as their mothers do, but still routinely nurse (Owen-Smith 1988). Calves 24 months of age and older are still found in association with their mothers, usually until the birth of her next calf (class D); calves in this oldest age category are nutritionally independent from their mothers, although they still may require protection from predators and conspecifics. When dates of births were unknown ($n = 11/21$), ages of calves were estimated based on size and horn development (Hillman-Smith et al. 1986) relative to calves of known ages.

Using radiotelemetry to locate animals, each mother–calf dyad was approached on foot and observed for 1–3 h; observations continued until the dyad was alerted to the presence of

the observer, at which time data collection was terminated. Observations were made during the first 3 h after sunrise and last 3 h before sunset, which represent the periods of peak activity for white rhinoceros (Owen-Smith 1973). The frequency and number of hours of observation for each female-calf dyad for each calf age class varied (daughters [$n = 9$]: A = 62 h, B = 161 h, C = 271 h, D = 43 h; sons [$n = 12$]: A = 45 h, B = 114 h, C = 619 h, D = 300 h). The reduced number of hours of observation for the oldest age class of daughters is largely due to shorter associations between mothers and daughters in this study. During observation sessions we recorded interactions between mother and calf using focal-animal sampling (Martin and Bateson 1993).

Behavioral measures.—Behavioral data were collected between October 2000 and October 2003. The following behaviors were recorded as events using all-occurrence sampling: 1) Suckling solicitation. Calves emit a whine vocalization, a thin mewling tone rising and falling in pitch, before suckling (Owen-Smith 1973, 1988). This vocalization was almost invariably associated with approach of the mother by the calf, particularly toward the teats. 2) Maternal response. Females often had to stop ongoing activities to allow the calf to suckle. If the mother enabled calf suckling within 2 min of a suckling solicitation, "maternal response" was recorded. 3) Suckling. This behavior was recorded when the calf's mouth was in the vicinity of the teat and either the calf was seen to grasp the teat in the mouth, make jerky head movements associated with suckling, or gulping sounds were heard. The duration of suckling was recorded. A suckling bout was terminated when the calf stopped suckling and did not continue another suckling episode for more than 2 min. Suckling occurred and was recorded in the absence of nursing solicitations. 4) Terminate suckling. Mothers or calves were considered to terminate suckling if 1 moved and broke contact with the other. We considered offspring to be weaned when suckling was no longer observed.

Although suckling behavior can be an unreliable indicator of milk transfer (Cameron 1998), we chose this as our measure of maternal investment for several reasons. First, weight measurements of wild rhinoceros mothers and calves are not feasible. Second, frequent nipple contact can inhibit reproductive cycling even when no milk is transferred (Gomendio 1989; Lee 1987). Finally, nonnutritive suckling can serve to comfort offspring and can therefore reflect differences in investment. Thus, although suckling behavior may not accurately measure milk transfer, differences in suckling behavior and maternal response may still be a reliable proxy for investment.

This research was approved by the Zoological Society of San Diego's Institutional Animal Care and Use committee and follows the guidelines of the American Society of Mammalogists (Animal Care and Use Committee 1998).

Data analysis.—To investigate how investment in offspring changed across the period of dependency and to test for differential investment in sons and daughters we used a mixed-model repeated-measures analysis of variance (SAS Institute Inc. 1993). This procedure was used because some data on offspring in different age classes were missing because of nat-

TABLE 1.—Number of births of white rhinoceros calves during the study period (1999–2003). Dry season months are April through September.

	Jan.	Feb.	Mar.	Apr.	May	Jun.	Jul.	Aug.	Sep.	Oct.	Nov.	Dec.
Males	3	1	1	1	0	4	1	4	3	2	1	4
Females	2	1	5	2	0	1	1	0	1	4	0	3
Total	5	2	6	3	0	5	1	4	4	6	1	7

urally variable lengths of mother-calf associations and the life of radiotransmitters. Additionally, some early age classes were missed when transmitters were installed in mothers with existing calves. Individual calves ($n = 21$) were used as a random effects variable (with age of calves as the within-subject measure) and sex of calves (between-subject variable) treated as a categorical fixed effect. Behavioral data collected on each calf were averaged within each age class, such that each calf contributed only 1 datum per age class. Because some mothers were used repeatedly in this analysis, we included mother as a random effect in the model nested within calf. Covariance parameters were estimated using restricted maximum likelihood and the denominator degrees of freedom were corrected using the Satterthwaite method (Kuehl 2000). Wald tests were used to determine the significance of the model terms for the fixed effects. Contrasts were generated for all sex by age interactions.

We used G -tests to compare the frequency of births related to season, adjusting for small sample sizes using the Williams correction (Sokal and Rohlf 1995). All other data were analyzed using 2-sample t -tests. Means and standard errors are reported for all data analyzed. Significance was set at the 0.05 level, but all P -values less than 0.10 are reported.

RESULTS

A total of 25 male and 20 female calf births were recorded during the study from individually recognizable females and females with transmitters. Calves were born throughout the year (Table 1). The average gestation period for the white rhinoceros is 16 months (Owen-Smith 1988) and thus conception and birth can occur in the same season (e.g., wet, wet) or in alternative seasons (e.g., wet, dry). Although more calves were born during the wet season ($n = 27$) than the dry season ($n = 18$), this difference was not significant ($G_{adj} = 1.79$, $d.f. = 1$, $P > 0.10$). Mothers had a nonsignificant tendency to produce more sons than daughters in the dry season ($G_{adj} = 3.58$, $d.f. = 1$, $P < 0.10$). Sons and daughters were produced with equal frequency in the wet season ($G_{adj} = 0.33$, $d.f. = 1$, $P > 0.50$). Average intercalving interval after the birth of a son (34.2 ± 5.3 months, $n = 14$) tended to be longer than the average intercalving interval after birth of a daughter (30.0 ± 5.5 months, $n = 7$) although this result was not significant (unpaired t -test: $t = 1.873$, $d.f. = 19$, $P = 0.08$).

Resource extraction.—Both the number of suckling bouts initiated per hour ($F = 49.11$, $d.f. = 3, 29$, $P < 0.0001$; Fig. 1a) and the percent time calves were observed suckling ($F = 31.03$, $d.f. = 3, 39$, $P < 0.0001$; Fig. 1b) varied significantly with calf

age. In support of the TWH, sons initiated significantly more suckling bouts ($F = 5.17$, $df = 1, 29$, $P = 0.03$; Fig. 1a) and spent significantly more time suckling ($F = 4.87$, $df = 1, 29$, $P = 0.04$; Fig. 1b) than did daughters. This effect appeared most pronounced during the youngest age class ($F = 11.25$, $df = 1, 29$, $P = 0.002$ for suckling bouts; $F = 7.89$, $df = 1, 29$, $P = 0.009$ for percent time suckling). Although suckling behavior was still observed in the oldest age class of sons, it was not observed in daughters of comparable age (Fig. 1). Consequently, males were significantly older at weaning (27.2 ± 2.2 months) than were females (19.1 ± 0.9 months; $t = 2.388$, $df = 10$, $P = 0.04$). Differences in suckling frequency were not compensated for with differences in suckling duration. The average duration of individual suckling bouts was surprisingly consistent across all age classes ($F = 1.53$, $df = 3, 26$, $P = 0.231$) where suckling was observed and did not differ between the sexes ($F = 0.36$, $df = 1, 26$, $P = 0.553$; Fig. 1c).

Offspring signaling and maternal responsiveness.—The frequency of suckling solicitations by calves appeared to decrease with calf age, although this effect was not significant ($F = 1.92$, $df = 3, 29$, $P = 0.148$; Fig. 2a). We found no difference in the frequency of solicitations between the sexes ($F = 0.04$, $df = 1, 29$, $P = 0.843$; Fig. 2a). Contrary to the predictions of sex allocation theory, a mother's response to the vocalizations of her offspring appeared largely unaffected by the age ($F = 1.36$, $df = 3, 24$, $P = 0.278$) or sex ($F = 0.43$, $df = 1, 24$, $P = 0.520$) of the calf (Fig. 2b), although there was a nonsignificant tendency for mothers to respond more to sons than to daughters of the youngest age class ($F = 3.45$, $df = 1, 24$, $P = 0.08$). Additionally, although the oldest age class of daughters was heard vocalizing, no suckling behavior was observed (Fig. 1). Mothers were responsible for terminating less than 20% of all suckling bouts in each age class ($F = 2.00$, $df = 3, 26$, $P = 0.138$) and they were equally likely to terminate suckling bouts for sons and daughters ($F = 0.00$, $df = 1, 26$, $P = 0.945$; Fig. 2c).

Offspring signaling of need.—For sons, the frequency of vocalizations was significantly correlated with the total number of suckling bouts (Spearman rank correlation: $r = 0.67$, $n = 21$, $P = 0.003$; Fig. 3a). In contrast, the total number of suckling bouts by daughters was statistically unrelated to the frequency of their solicitations ($r = 0.36$, $n = 17$, $P = 0.151$; Fig. 3b). Because, overall, mothers responded equally to the individual suckling solicitations of sons and daughters, these differences cannot be attributed purely to differential response by the mother.

DISCUSSION

Individual variation in the breeding success of males is high in white rhinoceros because more-competitive males are able to defend territories where they monopolize access to females (Owen-Smith 1973, 1988; Rachlow et al. 1998, 1999). The higher reproductive success of territorial males is supported by behavioral observations (Owen-Smith 1973; R. R. Swaisgood, in litt.) and molecular paternity analysis (Kretzschmar 2002). In

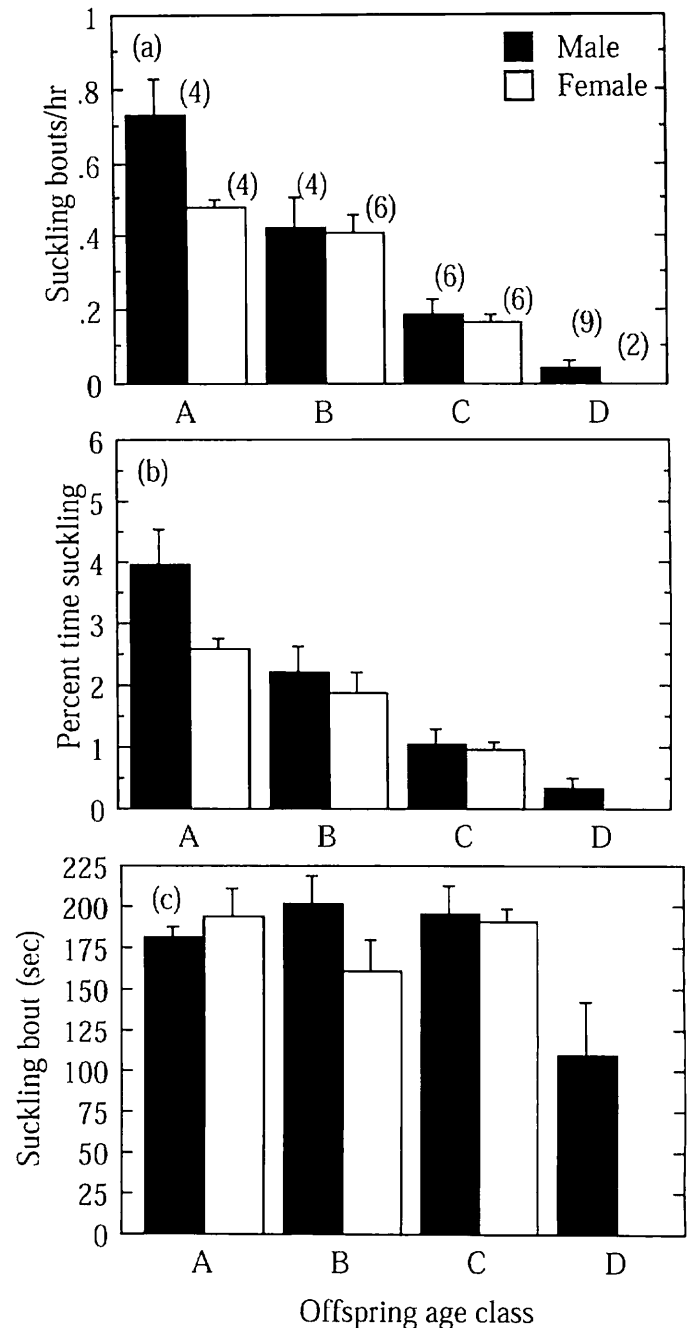


FIG. 1.—a) Number of suckling bouts per hour, b) percent time suckling, and c) length of suckling bout by male and female calves across age classes. Means and standard errors are shown. Sample sizes are presented in a).

contrast, quality of females is probably less strongly correlated with offspring production because the long interbirth interval limits the number of offspring a female can produce in her lifetime. Thus, according to the TWH, white rhinoceros mothers should invest more in sons than daughters whenever this investment gives sons an advantage when competing for mates as an adult. Given the extremely favorable conditions prevalent at our study site and the generally good body condition of our subjects, we expected that white rhinoceros mothers in our study would invest more in sons than daughters.

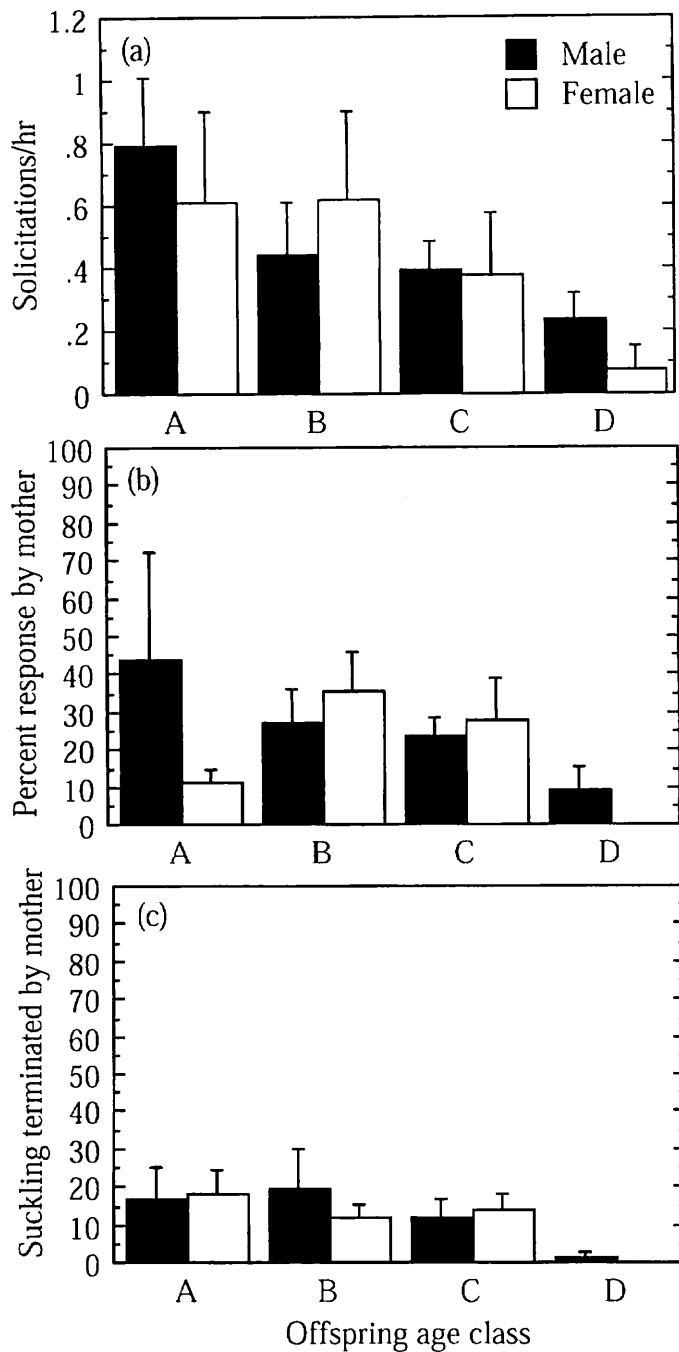


FIG. 2.—a) Number of nursing solicitations per hour by male and female calves across age classes. b) The percent of nursing solicitations in which the mother permitted suckling. c) The percent suckling bouts terminated by the mother in response to male and female calves across age classes. Means and standard errors are shown. Sample sizes are presented in Fig. 1a.

Our findings indicate that sons received increased investment compared to daughters. Specifically, mothers tended to have longer interbirth intervals after the birth of sons than daughters, sons initiated significantly more suckling bouts than daughters, sons spent significantly more time suckling than daughters (particularly in the earliest age class), and sons were significantly older than daughters at time of weaning.

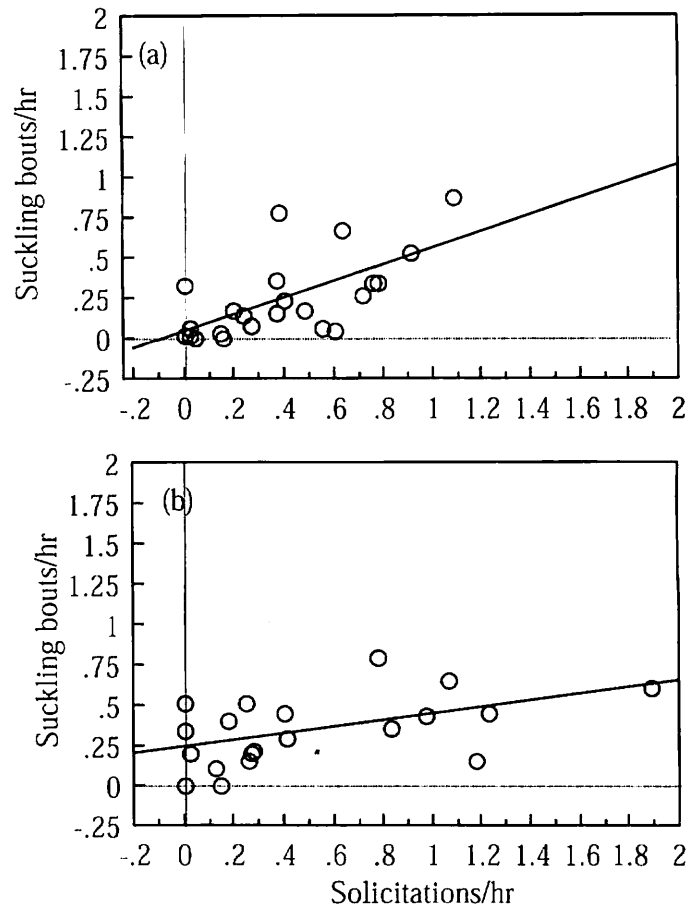


FIG. 3.—Relationship between solicitations by offspring for nursing and suckling rate in a) male and b) female calves.

Although initiation of suckling may seem to be under offspring control, we cannot rule out the possibility that initiation is influenced by the mother's history of response. The duration of suckling clearly requires the cooperation of both mother and offspring and, hence, should reflect maternal investment. As predicted by the TWH, white rhinoceros sons received higher investment than did daughters under favorable environmental conditions. Both mothers and sons stand to benefit from this increased investment. Mothers could increase their lifetime reproductive success by allocating more resources to a high-quality son and males could increase their reproductive chances by extracting additional resources from their mother.

Examination of these data reveals greater investment in sons during the early, most vulnerable stages of postnatal development and again at the end of the maternal investment period. This increased investment may enhance the chances of sons surviving and maintaining good condition postindependence. Poor condition during this period of uncertain access to resources, social instability, changing ranging patterns, and new and increased risks could set an animal on a trajectory toward poor adult body condition and low reproductive success. For example, Festa-Bianchet et al. (1994) found that early weaning in bighorn sheep negatively affected the growth of sons but not that of daughters. Given the age and decreased frequency of suckling during late stages of development, it is

possible that this suckling is nonnutritive. Even so, this suckling may represent a reproductive cost to mothers because it may delay or detract from future investment. Although not significant, interbirth intervals were longer after the birth of sons than daughters, suggesting costs to future reproduction as a consequence of increased investment in sons; this reproductive cost would likely be greater for mothers in poor condition.

Many studies are unable to determine if differences in resources received by sons and daughters are due to differential extraction by offspring or differential allocation by mothers (Brown 2001; Clutton-Brock 1991). We chose to study vocal solicitations for suckling by offspring and associated maternal response to determine whether patterns of differential investment were under maternal or offspring control. We did not find consistent support for maternal manipulation of investment. Suckling solicitations did not differ with sex of offspring and, more importantly, mothers were no more likely to respond to solicitations by sons, suggesting there is no maternal manipulation of resources. However, several possible exceptions to this interpretation were evident. For example, for calves in the youngest age class, mothers tended to respond more to solicitations from sons. Further, mothers failed to respond to vocalizations from the oldest age class of daughters, yet remained responsive to sons in this age class. Thus, our results are somewhat ambiguous regarding whether differential allocation was influenced by maternal manipulation of resources.

Among sons, those vocalizing at higher rates obtained more nursing bouts; among daughters, there was no statistical relationship between vocalization rate and number of nursing bouts. This pattern suggests that mothers respond differentially to solicitations for nursing from sons and daughters, which seems contrary to our finding that mothers are equally likely to respond to solicitations from offspring of both sexes. However, the 2 data sets are different in nature. The 1st analysis shows that, in response to individual vocal solicitations, mothers respond similarly to sons and daughters. The 2nd analysis shows that sons that vocalize at higher rates obtain more nursing bouts from the mother, whereas nursing bouts by daughters are unaffected by their rate of vocal solicitations. These analyses suggest that mothers allow more suckling from more-demanding sons, but not more-demanding daughters.

A potential limitation in our study of maternal investment (and most others on mammals) is that suckling behavior may not correspond directly to milk transfer, which is the primary currency of investment (although time and opportunity costs may also apply; reviewed in Cameron [1998]). Lactation is energetically demanding and can reduce maternal body condition and future reproductive success (Clutton-Brock et al. 1989). However, in our study, the consistency of suckling bout length between the sexes and across all age classes may indicate that, in white rhinoceros, the frequency of suckling is a suitable indicator of milk transfer. Additionally, in our study, differences in suckling behavior and maternal response indicate differential treatment of offspring related to their sex regardless of whether suckling behavior accurately measures milk transfer.

Another potentially confounding factor in many studies of differential maternal investment is sex-biased dispersal. Exam-

ination of the limited data available on white rhinoceros suggests that dispersal may be female-biased (Owen-Smith 1973). If so, then mothers should invest more in daughters, an expectation that is counter to our results. If both sexes disperse, then increased investment in sons over a longer period may increase the probability of successful dispersal and territory attainment. This increased investment may be more important to sons than to daughters, because mortality of males is estimated to be higher for both subadult and adult males, presumably due to fighting-related injuries (Owen-Smith 1988). Thus, greater maternal investment in sons may prepare males for the increased risks and challenges resulting from the different reproductive strategies employed by the sexes, rather than from dispersal per se.

Finally, sexual size dimorphism—a common confound for male-biased maternal investment in many mammalian species—does not appear to explain our results. Several authors have noted that the larger sex requires more resources than the smaller sex (Clutton-Brock et al. 1985; Lee and Moss 1986), and hence sexual dimorphism in size may provide a more-parsimonious explanation for differential maternal investment than the TWH. Few published data exist on the weights of wild or captive white rhinoceros (Owen-Smith 1988). Although some males weigh more than the mean body weight for females, there is substantial overlap in size between the sexes and adult males are not conspicuously larger than adult females. Thus, the greater maternal investment received by sons does not appear to be required to support sexually dimorphic growth.

In this study, we addressed several problems associated with tests of sex-biased investment in offspring. Our findings indicate that sons receive increased investment compared to daughters and suggest that this differential investment is under partial maternal control. This is one of a few studies to investigate whether differential treatment of sons and daughters is a consequence of differential allocation of resources by the mother or differential extraction of resources by the offspring. The TWH predicts that mothers can enhance their lifetime reproductive success by increasing investment in the more reproductively variable sex; at the same time, however, offspring may try to extract resources beyond the optimal level for the parent (Clutton-Brock 1991). Because lifetime reproductive success is rarely measured, sex-biased investment is only assumed to be reproductively beneficial to the mother. Alternatively, it may reflect a reproductive cost to the mother if offspring are extracting resources that could be better allocated to future siblings. Understanding the mechanism by which differential investment occurs is important in increasing our understanding of parental conflict and adequately addressing sex allocation theory. We suggest that more studies investigate whether sex-biased investment is maternally manipulated or is a consequence of the differential extraction of parental resources.

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