SEXUAL DIMORPHISM IN THE GREATER ONE-HORNED RHINOCEROS (RHINOCEROS UNICORNIS)

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ABSTRACT.—To assess sexual dimorphism in the greater one-horned rhinoceros (*Rhinoceros unicornis*), morphometric data were collected from 50 free-ranging individuals in Royal Chitwan National Park, Nepal. Twenty-two mensural and 16 nonmensural characters from 43 anesthetized individuals and seven carcasses, representing 4% of the entire wild population, provided the basis for this analysis. Adult males and females differed significantly in only a few of the mensural characters. Adult males developed significantly longer mandibular incisors and significantly greater neck musculature than females. Long incisors (rather than horns), powerful neck and shoulder musculature, and extensive neck and shoulder skin folds figured prominently in fights and displays between breeding-age males. Males born in zoos often are >25-cm taller at the shoulder and considerably larger in mass than females. Reduced size dimorphism in free-ranging animals, as observed in this study, may be explained by greater stress on males and poor nutrition during the long nonbreeding interval when young adults are harassed by dominant males and are excluded from prime grazing areas.

The extant Perissodactlya (rhinoceroses, tapirs, and horses) are typified by large body mass and the appearance of near monomorphism (Berger, 1986). One of these species, *Rhinoceros unicornis*, is the second largest rhinoceratid and the fourth-largest extant terrestrial mammal (Owen-Smith, 1988). Adult males may exceed 2,000 kg, although most published data on body mass of *R. unicornis* are from captive-born animals or are anecdotal for wild individuals. Among the other rhinoceratids, free-ranging black rhinoceroses (*Diceros bicornis*) show no difference in body mass (Freeman and King, 1969), male white rhinoceroses (*Ceratotherium simum*) are estimated to be ca. 28–41% heavier than females (Owen-Smith, 1988), and wild-caught adult Sumatran rhinoceroses (*Dicerorhinus sumatrensis*) show no obvious size dimorphism (T. Foose, pers. comm.; M. Dee, pers. comm.). No data exist for Javan rhinoceroses (*R. sondaicus*).

Mensural data are relatively scarce for *R. unicornis* despite the widespread slaughter of free-ranging animals during the last century and the presence of ca. 74 *R. unicornis* in captivity (Groves and Chakraborty, 1982; Laurie, 1978). Herein, I provide dimensional data on wild *R. unicornis* to examine the degree of sexual dimorphism within several age classes. I present criteria for determination of age and sex based upon physical attributes, dental wear, and other features observed on anesthetized individuals. Finally, I comment on the degree of sexual dimorphism observed in free-ranging and captive individuals as it relates to reproductive biology and social organization.

METHODS

Between 1984–1988, I measured 50 *R. unicornis* representing about 13% of the Royal Chitwan National Park population and 4% of all free-ranging individuals (Dinerstein and McCracken, 1990). Individuals measured were anesthetized with etorphine hydrochloride (Dinerstein et al., 1990). Thirty-six adults (20 males, 16 females) were measured and 18 (10 males, eight females) were fitted with radiocollars to facilitate field research on seed dispersal (Dinerstein, in press; Dinerstein and Wemmer, 1988), activity budgets, social organization, and breeding biology (Dinerstein et al., 1988; Dinerstein and Price, in press). Fights between breeding males resulted in early signal failure; replacement of transmitters allowed the opportunity to reexamine and remeasure seven adult males and two adult females. I measured six subadults (two males, four females) before their translocation to other reserves and six calves (two males, four females) before shipment to zoos. I also measured carcasses of four adult males, one subadult male, and two <1-year-old calves.

Ten characters were measured with cloth tape: total length of body; length of tail; length of head and body; maximum skull circumference; chest circumference; neck circumference behind head; neck circumference in front of shoulder; shoulder height; distance between junction of posterior cross-skin fold and anterior edge of anal skin fold; and horn circumference at base. Thirteen characters required use of tree calipers: length of hind foot to base of middle hoof; length of hind foot to tip of middle hoof; length of ear; length of head; cranial breadth; width behind head; width in front of shoulder; shoulder width; width across anterior cross-skin fold; width across posterior cross-skin fold; length of horn; length of lower left outer incisor; and length of lower right outer incisor. Complete data on all 23 characters are lacking for some individuals because I added several of these measurements after the 1st year. Shoulder height and chest circumference could be measured precisely only on translocated animals, which could be moved from sternal into lateral recumbancy during handling, or on carcasses.

Assessment of degree of dimorphism throughout the lifespan of wild *R. unicornis* required classifying anesthetized individuals or carcasses into discrete age classes. However, data are lacking on known-age, captive, or wild *R. unicornis* to link age with annual phenotypic changes.

I considered animals to be calves until they separated from the mother, at about 4 years of age, and subadults to consist of the age class from 4 to ≤6 years of age (Dinerstein and Price, in press). Thus, I was able to assign individuals to annual age classes based upon date of birth to 6 years of age. For adults (animals >6 years old) I relied partly on degree of tooth wear to classify adults into age categories. From study of known-age *D. bicornis*, Hitchins (1978) and Goddard (1970) identified 11 discrete age classes for adults based on cementum lines, and eruption and attrition of dentition. Studies of *C. simum* showed good correlation between known-age animals and cementum lines (Hillman-Smith et al., 1986) and researchers identified 16 tooth-wear classes with eight classes covering the adult age category. Because I was not able to examine cementum lines in M1 teeth of known-age adults, I instead modified techniques of Hillman-Smith et al. (1986) for creating age criteria based upon attrition of the molars. I established three adult age classes. I considered presence of sharp ridges on the lower molars to characterize the young adult class, a relative flattening of the ridges of lower molars to typify intermediate-aged adults, and well-formed depressions on the occlusal surface to indicate old adults.

Observations of captive animals in zoos revealed that old adults also can be distinguished easily from younger animals by size and by the accumulation of several nonmensural characters. Thus, I linked data on dentition with other mensural and nonmensural data to classify adults as either young, intermediate-aged, or old. Mensural characters included horn growth and size, body size, and length of mandibular incisors. Nonmensural data included wrinkles and development of secondary skin folds, erosion of tissue around the horn, and for females, the number of calves raised. In the process of establishing criteria for assigning adults to relative age classes, I assumed that wild animals should not differ from zoo animals in direction of accumulation of physical characters associated with advanced age (horn wear, wrinkles, and added skin folds), but perhaps only in magnitude. Also, I observed that horns grow at the rate of 2 cm/year in subadults and young adults and assumed that horns continue to grow at this rate until past middle age. Ages of old animals with broken horns were estimated by use of other characters.

To test for differences in mensural data between age and sex classes, I used a Mann-Whitney U-test. To test for differences in nonmensural characters among sex and age classes, I used chi-square analysis. I also analyzed variation in nonmensural characters for animals observed but not anesthetized during this study. I included such animals only if a complete set of photographs or detailed descriptions were available (Laurie, 1978).

RESULTS

Description of relative age categories for adults.—I constructed three age categories for adults based largely on dental condition and horn length, and I related these features to other nonmensural characters. Young adults possessed sharp occlusal ridges on lower molars, and lower outer incisors were <5.0 cm long and <3.0 cm wide at the base (males only). The horn was intact, with no erosion around the base, and short (<15.0 cm for females; <18.0 cm for males). Young adults had few or no scars and ears were usually without cuts (females). Young adults developed small secondary shoulder and neck folds and were relatively small in size.

Intermediate-aged adults showed moderate wear on the occlusal surface of the lower molars with mandibular outer incisors 4–5 cm long and >3.0 cm at base (females) and more elongated in males (range, 4.5–8.7 cm). Horns showed moderate erosion at the base and were 20–28 cm

long in females and 20–34 cm long in males and mostly entire. Circumference at the base of the horn was 48–54 cm for males.

Intermediate-aged adults were greater in length and girth than most young adults. Males showed extensive development of neck, shoulder, and secondary shoulder skin folds and thick upper-neck muscles. Males and females occasionally had cuts or pieces missing in one ear, but rarely both. Both sexes had moderate wrinkles around the mouth, under the zygoma, and around the eyes and forehead. Deep scars on anal folds, face, and back of legs were uncommon. A female nursing its second calf that had successfully weaned its previous calf was considered an intermediate-aged animal.

Old adults had heavy wear on the molars with well-formed depressions on the occlusal surface. Lower outer incisors were 4–5 cm long and >3.0 cm at base (females) and elongated in males (range, if entire, 5.1–8.9 cm) or often broken. The horn was either long (20–33 cm) or broken and heavily worn and eroded, often with deep anterior and occasionally posterior grooves. In males, horn base was large in circumference (55–95 cm), commonly with signs of breakage and subsequent regrowth. Old males developed extensive neck, shoulder, and secondary shoulder skin folds, and thick upper-neck muscles. Old adults had deep wrinkles around the mouth, under the zygoma, and around the eyes and forehead. Scars were prominent around the anal folds and backs of legs, and often there were major scars on the second cross-skin fold and minor scars on the face and other areas. Shoulder girdles, hip girdles, and ribs were prominent in old females. Old adults often had cuts or pieces missing in one ear and occasionally both. Unlike young and intermediate-aged males, old males seldom ran from humans riding on domesticated elephants (*Elaphas maximus*), and most old males squirted urine back between their legs in a dominance display.

Variation in measurements of adults relative to age and sex.—Dimensional data on young-adult males and females showed considerable overlap. Samples were too small to detect differences so I combined sexes for this category. The combined data show that young adults are noticeably smaller than intermediate-aged and old adults, indicating that females are reproductively active while still growing (Table 1).

No significant differences were found for any of the 23 characters between intermediate-aged and old males ($n = 8$ and 8, respectively) or between intermediate-aged and old females ($n = 4$ and 5, respectively). Thus, to increase samples for comparisons between the sexes, I combined data within each sex and renamed the combined category as older adults. For males this new classification parallels breeding activity; males classified as young adults did not breed in my intensive study area between 1984–1988. Among older adults, males were significantly larger than females in neck circumference behind head (Mann-Whitney $U = 112$, $n = 9$ and 13, $P < 0.001$), neck circumference in front of shoulder ($U = 106$, $n = 9$ and 13, $P = 0.001$), maximum skull circumference ($U = 79.5$, $n = 9$ and 11, $P < 0.005$), and width behind head ($U = 63.5$, $n = 7$ and 11, $P < 0.05$). Differences approached significance levels ($P < 0.10$) for cranial breadth and for width in front of shoulder. Larger neck measurements in breeding males are attributed to the greater muscle mass and enlarged skin folds around the neck (bibs). Radiocollared breeding males all required substantially larger collars than did females. Larger samples probably would show that older males are taller than females at the shoulder ($U = 9$, $n = 4$ and 3, $P = 0.10$), but chest circumference may prove to be more variable. Older males were slightly longer in length of head and body than females, but not significantly so.

Broken incisors were observed in four of the eight older males. If individuals with broken incisors are removed from the sample of older males, then males have significantly longer lower outer incisors than females as measured by the longer of the two incisors ($U = 109$, $n = 9$ and 13, $P < 0.001$) or by the mean length of the pair of intact incisors ($U = 112$, $n = 9$ and 13, $P < 0.001$). In contrast, lower outer incisors of young-adult females are as long as or longer than incisors of young-adult males. Horn circumference at base also was significantly larger in males ($U = 93.5$, $n = 9$ and 11, $P < 0.001$). Length of horn was roughly equal (Table 1). Subadults (4 to ≤6 years of age) could be distinguished readily from young adults by smaller size and shorter length of horn (Table 1).

TABLE 1.—*Univariate statistics for physical characteristics (in cm) of calves, subadults, young adults, and older adult Rhinoceros unicornis measured in Royal Chitwan National Park, Nepal, 1985–1988.*

Character	Calves <1 year old			Subadults			Young adults			Older adult males			Older adult females		
	n	X̄	SD	n	X̄	SD	n	X̄	SD	n	X̄	SD	n	X̄	SD
Total length of body	7	185.3	37.4	6	351.2	14.3	10	386.8	12.0	15	411.7	20.6	9	399.2	24.7
Length of tail	7	34.1	3.2	6	56.5	7.0	10	63.4	3.7	15	65.7	5.1	9	63.9	10.0
Length of head and body	7	151.1	35.5	6	294.7	15.5	10	323.3	9.7	15	346.0	18.4	9	335.3	25.7
Length of hind foot to base of middle hoof	7	29.3	5.0	6	45.5	6.8	7	47.7	1.6	14	49.3	2.7	7	47.7	4.1
Length of hind foot to tip of middle hoof	7	32.9	3.4	6	51.2	3.4	7	51.4	2.4	14	55.6	4.0	7	53.1	4.1
Length of ear	7	16.0	1.9	6	24.2	1.3	10	25.0	1.0	15	24.7	0.9	9	25.9	1.7
Maximum skull circumference	7	89.4	15.0	6	138.5	8.1	9	151.9	9.9	10	170.7	10.5	9	157.0	8.2
Chest circumference	3	116.7	12.5	3	252.0	34.8	3	275.0	29.2	4	314.5	28.1	3	298.7	41.5
Neck circumference behind head	7	73.6	13.2	6	112.2	12.8	9	134.4	14.4	13	159.2	12.6	9	135.7	5.8
Neck circumference in front of shoulder	7	94.1	21.0	6	144.5	18.9	9	159.3	12.2	13	201.3	16.7	9	173.0	8.5
Shoulder height	3	72.7	2.6	4	155.8	18.8	3	150.3	21.9	4	172.3	14.2	3	149.3	14.7
Length of head	5	38.6	4.5	2	49.0	17.0	3	64.0	1.4	8	68.8	2.9	5	69.2	8.1
Cranial breadth	6	25.3	2.5	3	36.3	2.1	6	38.3	1.3	11	42.0	1.3	7	40.6	1.5
Width behind head	6	24.2	4.1	3	32.7	1.7	6	36.5	3.7	11	47.5	5.9	7	41.4	1.8
Width in front of shoulder	6	26.3	6.2	3	43.3	5.7	6	45.5	5.4	11	55.6	8.1	7	49.6	4.0
Shoulder width	5	34.8	6.1	3	44.7	10.0	6	38.3	1.2	11	67.2	11.6	7	59.7	4.0
Width across anterior cross-skin fold	5	43.2	7.3	3	73.0	7.1	5	78.2	5.8	8	86.1	5.2	7	86.6	3.7
Width across posterior cross-skin fold	5	41.0	7.8	3	74.3	3.9	5	80.8	5.0	11	87.4	4.1	7	90.3	6.4
Distance between junction of posterior cross-skin fold and anterior edge of anal fold	5	53.8	8.5	3	108.3	29.6	4	95.8	10.2	10	111.6	4.6	4	110.8	0.8
Length of horn				6	12.2	2.0	9	15.9	3.5	15	25.3	4.7	9	23.8	4.6
Horn circumference at base				2	41.5	1.5	7	43.3	5.2	11	59.0	12.0	9	46.2	3.0
Length of lower left outer incisor	5	0.8	0.3	6	1.2	0.6	9	3.0	1.7	16	5.4	2.7	9	4.2	0.7
Length of lower right outer incisor	5	0.8	0.3	6	1.3	0.5	9	3.0	1.8	14	5.6	2.4	9	4.4	0.8

TABLE 2.—*Proportion of individuals exhibiting various physical characteristics among adult age and sex classes of* Rhinoceros unicornis *studied in Royal Chitwan National Park, Nepal, 1985–1988.*

Character and sample size	Young females	Young males	Intermediate-aged females	Intermediate-aged males	Old females	Old males
n	39	32	33	23	27	36
Knobs on second cross-skin fold	0.18	0.06	0.30	0.22	0.44	0.28
Knobs on anal skin fold	0.08	0.06	0.27	0.22	0.26	0.28
Knobs elsewhere	0.05		0.03			0.08
Scars on first cross-skin fold	0.03		0.03	0.04		
Scars on second cross-skin fold	0.08	0.09	0.12	0.04	0.11	0.11
Horn broken off			0.06		0.15	0.31
Horn heavily eroded at base			0.15	0.04	0.59	0.19
Horn with longitudinal groove in front	0.08	0.13	0.45	0.43	0.56	0.39
Pigmentation					0.04	
First extra cross-skin fold	0.03					0.03
Second extra cross-skin fold	0.03	0.03	0.06		0.07	
Extra neck-skin fold (females only)	0.13		0.24		0.19	
One ear cut	0.03	0.13	0.15	0.22	0.15	0.53
Two ears cut		0.03				0.11
Tail tip missing or bent			0.12		0.11	0.06

Variation in physical characteristics.—Variation in easily recognizable nonmensural characters (e.g., epidermal knobs, extra skin folds, entirety of the horn and ears, and scarring) permitted rapid identification of individuals (Laurie, 1978); thus, I examined the relationship between these characters and sex and age. Despite overlap in most mensural characters, old males could be separated readily from intermediate-aged males in the field. Old males were far more likely to have cut, scalloped, or torn ears ($\chi^2 = 4.3054$, $d.f. = 1$, $P < 0.05$), broken horns, scars on the second cross-skin fold, and erosion of the horn at the base than intermediate-aged males (Table 2). No intermediate-aged males had broken horns. All of the oldest males showed some scars on their flanks, around the tail, or the rear-leg folds, a result of often intense fighting among dominant breeding males, and pronounced secondary shoulder and neck folds.

Old females were less likely to have cut, scalloped, or torn ears than males ($\chi^2 = 8.5479$, $d.f. = 1$, $P < 0.005$). Old females were more likely to have heavy erosion of tissue around the horns than intermediate-aged females although this difference only approached significance ($\chi^2 = 2.2432$, $d.f. = 1$, $P > 0.10$). However, erosion around the horn was one of a suite of traits (e.g., extensive old scars on the rear, heavy wrinkles on the face, length of horn, known age of previous calves) that helped to place females in the old or intermediate-aged classes.

Nearly one-half of all old adults developed a longitudinal groove in the horn (Table 2). Almost one-half of all old females developed epidermal knobs (length, 3–25 cm) on the posterior cross-skin folds. Epidermal knobs were significantly less common on young adults than on older adults ($\chi^2 = 7.2465$, $d.f. = 1$, $P < 0.01$), suggesting that they may appear as the animal ages. The proportion of adults in each age class with epidermal knobs on anal folds was about equal.

Only one individual, an adult male, had an extra anterior cross-skin fold; four adult females and three subadults had extra posterior cross-skin folds. The proportion of old adults with bent tails or with the tail tips missing was not significantly different. Only one old female had heavy pigmentation on her body, on the right forefoot. I also detected no difference in the age of an adult female in relation to possession of an extra neck fold (Table 2).

Adult sex ratio and degree of disfigurement of breeding-age males.—Intraspecific fighting was the major source of mortality for males during the 4-year field study (Dinerstein and Price, in press). Intermale combat is likely to be most intense in areas where the ratio between breeding-age males and females is close to or exceeds parity with males greatly overrepresented. Not surprisingly, the frequent fighting between breeding males resulted in disfigurement of many males and was manifest as torn, cut, or scalloped ears, and numerous scars. Older males in the western and Bandarjhola-Narayani areas showed much greater scarring and damage to the ears

than in the Sauraha population. Older males from the western population more frequently had bitten or torn ears than did older males from the Sauraha population ($\chi^2 = 13.4282$, $d.f. = 1$, $P < 0.001$). The ratio of adult males to females was only 0.66:1 in the Sauraha area, 0.93:1 in the west population south of the Narayani River, and 2.0:1 in the Bandarjola-Narayani area, suggesting that combat between males is more frequent and intense where females are relatively more scarce.

DISCUSSION

Aspects of breeding biology and foraging ecology in *R. unicornis* provide a background for understanding patterns of sexual dimorphism. Courtship in *R. unicornis* is among the most violent among mammals; males aggressively pursue females during long courtship chases (>2 km) and attack females with their incisors or ram into them in an attempt to subdue them. On one and possibly two occasions, females died from wounds suffered in attacks by males. Reports of females dying from internal injuries sustained during courtship also were recorded on at least two occasions in captivity (M. Dee, pers. comm.). During my study, a radiocollared dominant male killed a newborn calf that it had not sired. Females begin an estrous cycle again soon after the loss of a calf.

Also, male *R. unicornis* form dominance hierarchies, and tenure as alpha male is short in comparison with longevity (Dinerstein and Price, in press). The long mean interbirth interval (46 months) and the presence of <150 breeding-age females in the population indicate that breeding opportunities are probably few for individual males. Limited chances for copulation probably heighten aggressive behavior when a female cycles into estrus. Lastly, nonbreeding males seldom use the prime grazing areas dominated by the grass *Saccharum spontaneum*. Young-adult males are attacked by dominant males if they remain in areas where breeding females concentrate. In contrast, females may occupy such areas even as subadults and continue to occupy the maternal home range as an adult (Dinerstein et al., 1988; Dinerstein and Price, in press; Laurie, 1978).

Male *R. unicornis* can be 1,000 kg heavier and at least 25 cm taller than females in captivity (M. Dee, pers. comm.). However, I never observed such extreme size dimorphism in free-ranging animals as reported for captive individuals (Lang, 1961). Body-mass data for males obtained for zoo animals must be viewed with caution. Males born in captivity may become much larger than captive-born adult females after only 4 years. In the wild, 4-year-old males are always substantially smaller than adult females. Three of the nine older females measured in this study had greater length of head and body and appeared almost as large as the males that bred them. Larger samples most likely will show that old adult males are probably taller at the shoulder and slightly heavier than most old females. However, slight differences in body mass may not be a critical dimorphic feature in species whose adults exceed 1,500 kg. For free-ranging *R. unicornis*, I suggest that adult males are essentially a slightly larger version of females, and that the most conspicuous differences in morphometrics are directly related to the dental weapons and the enlarged neck and shoulder musculature of males, relied upon during the frequent intermale fights that determine dominance and access to estrous females.

Elongation of the incisors may be under control of androgen levels in *R. unicornis* as is dimorphism in canine length for some primates (Zingeser and Phoenix, 1978). *R. unicornis* males slash and gouge one another with the razor-sharp lower outer incisors during fights to determine dominance rather than relying on the horn. Three dominant males in Royal Chitwan National Park maintained their status with broken horns but intact incisors.

Dimorphism also is observed in the massive neck and upper shoulder muscles, which are more extensively developed in adult males. These muscles provide the force behind the slashing and gouging with the incisors. The extensive primary and secondary neck and shoulder folds found in dominant males may serve for display in head-on confrontations between rival males, and to deflect the penetration of an opponent's incisors from the neck, chest, and shoulder area. This is the region where most severe attacks first occur before one male inevitably turns and runs

from the the other. *R. unicornis* is believed to have poor eyesight, but the head-on display, which often precedes combat, occurs when males are within a few meters of one another. Presentation of the large neck and shoulder skin folds and baring of the outer incisors during display may cause a challenger to submit and flee before the encounter with the dominant male intensifies into a fight.

Female *R. unicornis* often have horns longer (though slightly narrower) than do males that breed them. All three species of rhinoceroses occurring in Asia possess elongated lower outer incisors, but these are smaller in *R. sondaicus* and *D. sumatrensis*. In contrast, the two African species lack lower outer incisors and fight and display exclusively with the horns.

Reduced size dimorphism of wild *R. unicornis* may result from forces operating on both males and females. There may be selection for large females, as larger females would be better able to defend themselves and their offspring against males, a special case of the "big mother" hypothesis (Ralls, 1976). More likely, growth of wild males often may be restricted by poor nutrition and behavioral factors. Stunted growth for some males may be related to reduced protein intake during the long period of adolescence. Males occupy marginal habitats offering less-often-selected forage during the nearly 10-year period between when males are physiologically capable of breeding (ca. 5 years) and when they actually associate with females on prime grazing areas (at about 12–15 years of age). Stress associated with frequent harassment and attacks by breeding males on younger males also may result in free-ranging males failing to reach the large sizes and accentuated dimorphism observed in captivity, where males are held separately. Data for several mammalian species show that size of adult males is reduced more severely than size of adult females if food resources are curtailed during the normal period of rapid growth (Ralls and Harvey, 1985; Widdowson, 1976; Wolanski, 1979). The upper limit of body size in *R. unicornis* presumably is determined by genetic factors, but comparison of observations of free-ranging and captive individuals implicate diet and behavior in influencing the degree of dimorphism in body mass and other dimensional data in this species.

ACKNOWLEDGMENTS

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