

## TREE RUBBING BY WHITE RHINOS: POTENTIAL FUNCTIONS OF AN UNDESCRIBED BEHAVIOR

Janet L. Rachlow<sup>1</sup>

Ecology, Evolution, and Conservation Biology, University of Nevada Reno, Reno, NV 89512, USA

**ABSTRACT:** I observed white rhinos (*Ceratotherium simum*) in Matobo National Park, Zimbabwe, perform a behavior previously undescribed for this species; males vigorously removed the bark from commiphora trees (*Commiphora marlothii*) with their horns, and then rubbed their head and rostrum on the debarked areas. To explore this behavior further, I sampled commiphora trees in the Whovi Game Park, a fenced reserve within Matobo National Park, which contained a population of 43 white rhinos. Almost 30% of commiphora trees available to rhinos had been debarked. Only 2 marks were observed on 107 trees sampled outside the fenced reserve, in an area without a resident population of rhinos. Tree rubbing in white rhinos is similar to “sign-posting” in cervids and some bovids, and may function as a scent-marking behavior. Alternatively, perhaps rhinos ingested bark or resin during tree rubbing. Therefore, other potential functions of this behavior may include nutritional or medicinal use of commiphora.

ALCES VOL. 37 (2): 447-456 (2001)

**Keywords:** *Ceratotherium simum*, *Commiphora marlothii*, scent marking, sign-posting, tree rubbing, white rhinos, zoopharmacognosy

Rubbing of trees with the head and horns or antlers is a common behavioral activity in many species of ungulates. Often this behavior is preceded by removal of tree bark, creating a visual marker or “sign-post” (Bowyer and Kitchen 1987, Bowyer et al. 1994). Tree rubbing is believed to communicate olfactory information to conspecifics via pheromones deposited on rubbed trees (Müller-Schwarze 1972, Volkman et al. 1978, Macdonald and Brown 1985). This behavior is widespread in the Cervidae, and has been studied in North American elk (*Cervus elaphus*; Bowyer and Kitchen 1987), moose (*Alces alces*; Bowyer et al. 1994), caribou (*Rangifer tarandus*; Adams et al. 2001), and several species of deer including white-tailed deer (*Odocoileus virginianus*; Marchinton and

Hirth 1984, Benner and Bowyer 1988), mule and black-tailed deer (*O. hemionus*; Müller-Schwarze 1972, Bowyer 1986), roe deer (*Capreolus capreolus*; Johansson et al. 1995), and fallow deer (*Dama dama*; Massei and Bowyer 1999).

In moose and other cervids, tree-rubbing behavior involves antorbital and preorbital or lachrymal scent glands, which are located on the forehead and anterior to the eyes (Quay and Müller-Schwarze 1970, Atkeson and Marchinton 1982, Bubenik 1998). Similar deposition of secretions from scent glands onto vegetation is widespread in African antelopes and gazelles (Gosling 1985, Estes 1991). Modification of grasses or bushes prior to rubbing with the antorbital glands has been documented in oribi (*Ourebia ourebia*; Gosling 1972) and harte-

<sup>1</sup>Present address: Department of Fish and Wildlife Resources, University of Idaho, Moscow, ID 83844-1136, USA

beest (*Alcelaphus buselaphus*; Gosling 1985). Like cervids, male muntjacs (*Muntiacus reevesi*) strip bark from trees and bushes before rubbing them with their forehead glands (Barrette 1977). Rubbing of trees and other vegetation is one of a suite of scent-marking behaviors expressed by ungulates. Other marking behaviors involve scent glands located on the feet, tarsals, prepuce, and rump; associated behaviors include urination, defecation, digging, and wallowing (Gosling 1985, Moehlman 1985).

Scent-marking behaviors described for white rhinos (*Ceratotherium simum*) include spray-urination and ritualized defecation during which dung is scattered with the hind feet (Owen-Smith 1975). Those behaviors are performed exclusively by males and are associated with territoriality (Owen-Smith 1971, Rachlow et al. 1998). Scent glands have been described on the prepuce of white rhinos (Cave 1966) and urine of males is milky and odoriferous (Groves 1972). Although both black rhinos (*Diceros bicornis*) and white African rhinos wallow in mud and water, those behaviors are not accompanied by the release of urine and appear to be associated with parasite removal and thermoregulation (Schenkel and Schenkel-Hulliger 1969, Owen-Smith 1973). Pedal glands have been identified in *Rhinoceros*, which includes the Indian rhinos (*R. unicornis*) and Javan rhinos (*R. sondaicus*), but similar glands have not been described in African rhinos (Cave 1962). No other integumentary scent glands are known for any species of rhinos.

White rhinos rub their horns on trees, anthills, rocks, and other objects, but such behavior has not been associated with glandular secretions or proposed to function in scent marking (Owen-Smith 1973). Horn rubbing is performed infrequently by both sexes, although more often by males (Pienaar et al. 1991). Rates of horn growth

(Pienaar et al. 1991) and regrowth after dehorning (Rachlow and Berger 1997) also were higher in males than females. Horn rubbing results in visible wear on the lateral and anterior surfaces of horns; however, the function of this behavior is unknown (Owen-Smith 1973, Pienaar et al. 1991).

During field observations of white rhinos in Zimbabwe, I observed 2 occurrences of prolonged and vigorous rubbing of the horns, rostrum, and head on paperbark commiphora trees (also known as paperbark corkwood; *Commiphora marlothii*) that resulted in debarking large areas (64 x 15 cm and 107 x 21 cm) on the trunks. Although I occasionally observed rhinos rubbing their horns on other species of trees, those actions were not performed with the same intensity, duration, or resultant debarking as observed on commiphora. Subsequent observations revealed that many commiphora trees bore similar marks from debarking. In contrast, I did not observe comparable marks on other species of trees.

I examined the prevalence of "marks" on commiphora trees in Matobo National Park, Zimbabwe, in areas with and without rhinos. Objectives of this work were to quantify the marks observed on commiphora trees, to characterize marked trees, and to address the following questions: Were the marks a result of rubbing behavior by rhinos? If so, what are the potential functions of tree-rubbing behavior in this species?

### STUDY AREA

Fieldwork was conducted in Matobo National Park (20°30'S, 28°30'E), Zimbabwe, during 1994-95. The Park encompasses 425 km<sup>2</sup> of the rugged Matobo Hills in the southwestern part of the country. Granite domes and kopjes (outcrops or hills composed primarily of boulders) dominate the terrain, which is traversed by perennial and seasonal rivers. Vegetation within Matobo Park is a mosaic of woodlands,

grasslands, and riparian habitats. The most common vegetation type is woodland associated with the granite hills or kopjes. Dominant trees in the kopje woodland included *Ficus* spp., *Commiphora marlothii*, and *Euphorbia* spp. More open bushlands and grasslands resulting from historic cultivation occur in flat areas interspersed among rocky hills.

White rhinos were extirpated in most of southern Africa, including Zimbabwe, in the late 1800s. Beginning in the 1960s, white rhinos were reintroduced to Matobo National Park from Natal, South Africa. Translocated rhinos were released into the Whovi Game Park, a fenced reserve of 105 km<sup>2</sup> in the western portion of Matobo National Park (Rachlow and Berger 1998). Most white rhinos ( $n = 43$ ) in Matobo Park during this study inhabited the fenced Whovi Game Park. A smaller group ( $n = 9$ ) ranged over approximately 60 km<sup>2</sup> in the eastern reaches of Matobo National Park (Rachlow et al. 1999).

Other large ungulates common in the study area included Burchell's zebra (*Equus burchelli*), impala (*Aepyceros melampus*), giraffe (*Giraffa camelopardalis*), greater kudu (*Tragelaphus strepsiceros*), wildebeest (*Connochaetes taurinus*), waterbuck (*Kobus ellipsiprymnus*), sable (*Hippotragus niger*), klipspringer (*Oreotragus oreotragus*), common duiker (*Sylvicapra grimmia*), steenbok (*Raphicerus campestris*), warthog (*Phacochoerus aethiopicus*), bushpig (*Potamochoerus porcus*), and 12 black rhinos. Giraffes and rhinos were restricted to the fenced Whovi Game Park, but all other species occurred both within the fenced reserve and in the remaining area of Matobo National Park, outside the fence.

## METHODS

I conducted behavioral observations of white rhinos in Matobo National Park from

March 1994 through January 1995 (Rachlow and Berger 1998, Rachlow et al. 1999). Following 2 observations of rhinos debarking commiphora trees, I sampled commiphora to assess prevalence of trees with similarly debarked trunks. Because commiphora primarily are associated with the kopje woodlands, I searched kopjes in the study area for concentrations of this species. Once located, I circumvented the rocky hills to measure all commiphora trees associated with each discrete kopje that were potentially available to rhinos for rubbing. Trees were considered available to rhinos if they met one of the following criteria: (1) the tree grew on a level to moderate slope; or (2) the tree grew on a steeper or rocky slope, but was immediately adjacent to a rhino trail. White rhinos rarely were observed using steep, rocky terrain, except where they traversed such areas on well-worn footpaths. Therefore, when sampling commiphora, I excluded trees that were on steep or rocky slopes, unless they were immediately adjacent to a game trail. To determine whether rhinos were responsible for the prevalence of debarked commiphora trees within the fenced reserve, I located rock kopjes with concentrations of commiphora adjacent to, but outside of the fenced reserve, and sampled trees in the same manner. I measured a total of 110 trees on 5 kopjes within the fenced reserve and 107 trees on 4 kopjes outside the fence.

For each tree sampled, I measured the basal circumference and circumference at breast height (approximately 1.3 m above ground). Because commiphora were associated with rocky hillsides, I also recorded height of the tree base above flat ground surrounding the kopje. On debarked trees, I measured length and width of rubs, and height of the midpoint of the marks. I examined characteristics of trees selected for rubbing within the fenced reserve. Measurements from marked and unmarked

trees were contrasted using *t*-tests (Zar 1999). *P*-values were adjusted using the sequential Bonferonni correction for multiple comparisons (Rice 1989). Proportions of marked trees in the samples within and outside of the fenced reserve were contrasted using *Z*-tests (Zar 1999).

### RESULTS

In 1994, I observed 2 occurrences of tree rubbing and associated behaviors that have not been described previously for white rhinos. During the first observation on 25 September, a solitary adult male (M9) vigorously rubbed his horn, rostrum, and forehead on a commiphora tree for > 15 min. Bark was removed from a large area of the trunk (Fig. 1). Subsequently, the male pawed the ground and appeared to sniff and possibly feed around the base of the tree. On 13 October, I observed a different adult male (M25) forcefully debark a commiphora tree for approximately 5 min. The tree rubbing was preceded by chewing on a commiphora branch that was broken off of a nearby tree. Following tree rubbing, M25 also appeared to smell or feed around the tree. The shavings of bark that littered the ground were wet, presumably with nasal mucous or saliva; however, I could not determine if the bark was ingested.

These two observations shared several common characteristics. First, the green bark was removed from the commiphora trunk, leaving a rubbed area about 1.5 cm deep through the bark down to the wood. Copious amounts of highly aromatic sap were released from the debarked areas. Second, both males rubbed not only their horns, but also their mouths, rostrums, and foreheads on the trees. Close observation of 1 male (M25) following the tree rubbing revealed wet areas around the horns, eyes, and mouth, likely from sap released during debarking. Third, both behaviors were performed by males that were expanding the



Fig. 1. J. Gumede measuring a paperbark commiphora (*Commiphora marlothii*) in Matobo National Park, Zimbabwe, 1994. Evidence of recent (below) and older (above) debarking is apparent on this tree. The unmarked commiphora on the right shows the smooth bark typical of this species.

size of their territories following the death of a neighboring territory holder, and both of the tree-rubbing events were preceded by frequent spray-urination temporally interspersed with grazing. Last, both males appeared to sniff or feed around the base of the tree after debarking, which may have accompanied ingestion of some of the removed bark. The size (length x width) of the areas debarked during these two events was 64 x 15 cm and 107 x 21 cm, and the midpoints were 56 cm and 143 cm above the ground, respectively.

I measured 30 other commiphora trees with comparable marks on their trunks. In some instances, trees appeared to have been debarked repeatedly. Recent rubs were identified by the pale color of exposed wood and by the presence of an aromatic, sticky sap along the edges of marks. Older marks were characterized by darkened areas of exposed wood and healing of the

inner bark around the perimeter of the rub (Fig. 1). Measurements reflect the entire area debarked during past and more recent events. Dimensions ( $\bar{x} \pm SD$ ) of rubs within the Whovi Game Park were  $85 \pm 42$  cm in length (range = 15 - 226 cm) and  $16 \pm 10$  cm in width (range = 3 - 41 cm). Average height of the midpoint of the marks was  $86 \pm 21$  cm above the ground (range = 46 - 143 cm).

Commiphora trees that bore marks differed from unmarked trees in size and location. Within the fenced reserve, trees with rubs had significantly larger basal and breast-height circumferences than unmarked trees. Additionally, marked trees were closer to the ground level around the rock kopjes (Table 1).

No trees sampled outside the fenced reserve bore fresh marks similar to those on commiphora within the Whovi Game Park. Two of 107 trees sampled had older scars on the trunks that were comparable in size (64 x 8 cm and 100 x 5 cm). The remaining 105 trees in the sample lacked such marks. The proportion (0.02) of marked trees in the sample collected outside of the fenced reserve differed significantly ( $Z = 5.33$ ;  $P < 0.0001$ ) from that within the reserve (0.29).

## DISCUSSION

Vigorous debarking of trees followed by rubbing of the head that I observed in white rhinos in Matobo National Park has not been described for either species of African rhinos. Owen-Smith (1973) noted that white rhinos rubbed their horns against trees and other objects in the environment, but that such behavior was both gentle and infrequent. Similarly, horn rubbing by white rhinos was observed in Kruger National Park, South Africa, but did not result in debarking commiphora or other species of trees (D. J. Pienaar, personal communication). Schenkle and Schenkle-Hulliger (1969) likewise noted that horn rubbing was

Table 1. Characteristics of commiphora trees marked and not marked by white rhinos in the fenced Whovi Game Park within Matobo National Park, Zimbabwe, 1994-95.

	Marked			Unmarked			t	Corrected P - value <sup>1</sup>
	$\bar{x}$	SE	n	$\bar{x}$	SE	n		
Basal circumference (cm) <sup>2</sup>	57	5	21	41	3	57	-2.65	0.0097
Circumference at breast height (cm)	52	4	32	42	3	78	-1.99	0.0488
Height of base above ground (m) <sup>3</sup>	0.71	0.11	21	1.68	0.15	57	4.44 <sup>3</sup>	<0.0001

<sup>1</sup> Sequential Bonferroni test indicated table-wide significance at  $P < 0.05$ .

<sup>2</sup> Trees with multiple trunks growing from one base were deleted from analyses of basal circumference and height of base above the ground.

<sup>3</sup> The t-test for unequal variances is reported because variances differed from equality despite data transformations.

an infrequent behavior in black rhinos. Although rhinos in captivity commonly have short angular horns as a result of rubbing along walls, fences, and other barriers, such extreme wear is not evident in wild populations.

The hypothesis that the marks I measured on the commiphora trees in the fenced reserve were made by rhinos is supported by two lines of reasoning. First, marks were consistent in appearance, size, and location on the trunks with the marks made during observations of tree rubbing by white rhinos. Second, all of the common mammal species, except rhinos and giraffes, occur on both sides of the fence, and giraffes are not known to debark trees, especially near ground level. Prevalence of marks inside the reserve and the paucity of marks outside support the inference that the marks were a result of rubbing behavior by rhinos. Debarking trees has not been described for black rhinos, and the extent to which the 12 black rhinos in the fenced reserve may have contributed to the tree rubs is unknown.

Two trees sampled outside of the fenced reserve had old marks. Perhaps those marks were made when rhinos occasionally broke through the fence and roamed outside the reserve. Alternatively, a white rhino from the small group that inhabited the eastern portion of Matobo National Park may have moved as far west as the fenced reserve. Such movements did not occur during this study, but may have in the past.

Sampling for this study was restricted to commiphora because preliminary investigations indicated that other tree species were not marked in the same manner. Commiphora trees have a smooth, green bark and a highly aromatic sap. Selection of aromatic species for tree rubbing also has been recorded in white-tailed deer (Kile and Marchinton 1977, Miller et al. 1987, Oehler et al. 1995), roe deer (Johansson et al. 1995), fallow deer (Massei and Bowyer

1999), and moose (Bowyer et al. 1994). Trees marked by rhinos were larger and closer to the ground around the hillsides than unmarked trees. Size, smoothness of the bark, and height of the first branch above the ground also influenced selection of trees for rubbing by other ungulate species (Benner and Bowyer 1988, Bowyer et al. 1994, Johansson et al. 1995, Massei and Bowyer 1999, Adams et al. 2001).

Tree rubbing plays an important role in scent communication in cervids. Sign-posts made by North American elk are initiated by removal of tree bark with the incisors or antlers, followed by rubbing the head, neck, and shoulders onto the debarked area (Bowyer and Kitchen 1987). Similar behaviors are exhibited by moose (Bowyer et al. 1994) and North American deer (Müller-Schwarze 1972, Marchinton et al. 1990). In addition to creating a visual advertisement of the scent mark, debarking prior to rubbing may serve other functions. Modifying the vegetation may fashion a more effective surface for deposition of scent secretions. Such behavior also may accomplish self-marking, in which the scent is distributed around the horns or antlers and other parts of the head, as well as possibly anointing the animal with odors produced by the rubbed tree (Gosling 1985). Although the exact information communicated by tree rubbing in cervids is unknown and may vary among species, tree rubbing in these ungulates functions in scent marking (Bowyer et al. 1994), and may prime estrus in females (Whittle et al. 2000).

What are potential functions of tree-rubbing behavior in white rhinos? The similarity of the behavior to sign-posting in cervids and bovids suggests that scent marking is a possible function. Nonetheless, rhinos differ from cervids and bovids in important ways that bear on interpretation of this behavior. First, visual cues such as signposts likely play a limited role in com-

munication. Rhinos lack the excellent vision of most other ungulates, relying instead on acute senses of olfaction and hearing (Owen-Smith 1975). Use of highly aromatic tree species, however, may increase the effectiveness of a tree rub in drawing the attention of other rhinos. This idea has been forwarded previously to explain selection of aromatic species for tree rubbing in cervids (Bowyer et al. 1994, Johansson et al. 1995).

Another difference is that rhinos lack scent glands, which play a prominent role in tree-rubbing behavior of cervids. A scent gland in the facial region has not been described for any rhino species (Groves 1972). Hairs in all mammals, however, are associated with sebaceous glands, and as such, each hair has the potential to release and communicate olfactory information (Eisenberg 1981). Saliva also communicates socially important odors in many mammals, including several species of pigs (*Suidae*; Gosling 1985, Leus et al. 1996). Therefore, the lack of well-developed antorbital or frontal glands does not necessarily preclude scent communication as a function of tree-rubbing behavior in white rhinos. Although not accompanied by debarking, black rhino males have been observed to rub their head, snout, and horn bases on stumps and trees. Schenkle and Schenkle-Hulliger (1969) postulated that this activity may function in scent marking. The prolonged rubbing of the head and mouth on debarked trees by white rhinos supports the interpretation of tree rubbing in this species as a scent-marking behavior.

Although scent marking is a probable function of tree rubbing in rhinos, alternative hypotheses exist. In both observations of this behavior, rhinos appeared to sniff or feed around the base after rubbing the tree. Rhinos may have ingested bark removed during rubbing. Both observations of rhinos debarking trees were made at the end of the

dry season when forage quality and quantity were low. Although white rhinos are grazers, these large herbivores may derive a nutritional benefit from eating commiphora bark.

Alternatively, rhinos may have selected commiphora trees because of other properties. The growing body of literature about zoopharmacognosy, the use of medicinal plants by wild animals, suggests that many species use specific plants for medicinal purposes (Rodriguez and Wrangham 1993). The genus *Commiphora* is a member of the Burseraceae (or myrrh) family, which produces resins that have a long history of medicinal use by humans and potentially by wildlife (Gompper and Hoylman 1993). Resins are stored in special ducts or glands, but additional resin is produced when a plant is damaged (Ross and Brain 1977). Resin from *Commiphora* spp. is a masticant used by the Maasai and Batemi people of eastern Africa (Johns and Chapman 1995). Although not previously documented, rhinos may derive a medicinal benefit from the resins released during rubbing of commiphora.

Distinguishing among hypotheses about the function of this behavior is hampered by limited observations of tree-rubbing activity in white rhinos. Information about the spatial and temporal distributions of tree rubs, which individuals perform tree rubbing, and whether other rhinos respond to rubs is needed to understand the functional significance of this behavior. If tree-rubbing functions to communicate information via scent deposition, then conspecifics would be expected to investigate and respond to rubbed trees. If the information conveyed relates to territorial marking or defense, then only territorial males should perform tree rubbing. In contrast, if the behavior communicates information about reproductive status, then both sexes may perform tree rubbing. Diet analyses and additional

observations of this behavior would provide insights on whether rhinos ingest bark or resin, and potentially gain nutritional or medicinal benefits. Research addressing these issues is needed to test hypotheses about the function of this previously undescribed behavior in white rhinos.

#### ACKNOWLEDGEMENTS

I thank the Zimbabwe Department of National Parks and Wild Life Management for permission to conduct this research. Funding was provided by the Frankfurt Zoological Society and by the Program in Ecology, Evolution, and Conservation at the University of Nevada Reno. I appreciated the assistance of the staff at Matobo National Park, the Whovi Game Park scouts, M. Kock, M. Atkinson, S. Frick, and J. Frick. J. Gumede generously shared his time and knowledge of rhinos. I thank the Patullo and Doddman families for their hospitality. J. Witham, N. Owen-Smith, and an anonymous reviewer provided helpful comments on earlier drafts of this manuscript.

#### REFERENCES

- ADAMS, C., R. T. BOWYER, J. E. ROWELL, W. E. HAUER, and J. A. JENKS. 2001. Scent marking by male caribou: an experimental test of rubbing behavior. *Rangifer* 21:21-27.
- ATKESON, T. D., and R. L. MARCHINTON. 1982. Forehead glands in white-tailed deer. *Journal of Mammalogy* 63:613-617.
- BARRETTE, C. 1977. Scent marking in captive muntjacs, *Muntiacus reevesi*. *Animal Behaviour* 25:536-541.
- BENNER, J. M., and R. T. BOWYER. 1988. Selection of trees for rubs by white-tailed deer in Maine. *Journal of Mammalogy* 69:624-627.
- BOWYER, R. T. 1986. Antler characteristics as related to social status of male southern mule deer. *Southwestern Naturalist* 31:289-298.
- \_\_\_\_\_, and D. W. KITCHEN. 1987. Significance of scent-marking by Roosevelt elk. *Journal of Mammalogy* 68:418-423.
- \_\_\_\_\_, V. VAN BALLEMBERGHE, and K. R. ROCK. 1994. Scent marking by Alaskan moose: characteristics and spatial distribution of rubbed trees. *Canadian Journal of Zoology* 72:2186-2192.
- BUBENIK, A. B. 1998. Evolution, taxonomy and morphophysiology. Pages 77-123 in A. W. Franzmann and C. C. Schwartz, editors. *Ecology and management of the North American moose*. Smithsonian Institution Press, Washington, D.C., USA.
- CAVE, A. J. E. 1962. The pedal scent gland in *Rhinoceros*. *Proceedings of the Zoological Society of London* 143:569-586.
- \_\_\_\_\_. 1966. The preputial glands of *Ceratotherium*. *Mammalia* 30:153-159.
- EISENBERG, J. F. 1981. The mammalian radiations: an analysis of trends in evolution, adaptation, and behavior. University of Chicago Press, Chicago, Illinois, USA.
- ESTES, R. D. 1991. The behavioural guide to African mammals. University of California Press, Berkeley, California, USA.
- GOMPPER, M. E., and A. M. HOYLMAN. 1993. Grooming with *Trattinnickia* resin: possible pharmaceutical plant use by coatis in Panama. *Journal of Tropical Ecology* 9:533-540.
- GOSLING, L. M. 1972. Construction of antorbital gland marking sites by male oribi (*Ourebia ourebia*, Zimmermann, 1783). *Zeitschrift für Tierpsychologie* 30:271-276.
- \_\_\_\_\_. 1985. The even-toed ungulates: order Artiodactyla. Pages 550-618 in R. E. Grown and D. W. Macdonald, editors. *Social odours in mammals*.





- Claredon Press, Oxford, U.K.
- GROVES, C. P. 1972. *Ceratotherium simum*. Mammalian Species 8:1-6.
- JOHANSSON, A., O. LIBERG, and L. K. WAHLSTRÖM. 1995. Temporal and physical characteristics of scraping and rubbing in roe deer (*Capreolus capreolus*). Journal of Mammalogy 76:123-129.
- JOHNS, T., and L. CHAPMAN. 1995. Phytochemicals ingested in traditional diets and medicines as modulators of energy metabolism. Pages 161-188 in J. T. Arnason, R. Mata, and J. T. Romeo, editors. Phytochemistry of medicinal plants. Plenum Press, New York, New York, USA.
- KILE, T. L., and R. L. MARCHINTON. 1977. White-tailed deer rubs and scrapes: spatial, temporal and physical characteristics and social role. American Midland Naturalist 97:257-266.
- LEUS, K., K. P. BLAND, A. A. DHONDT, and A. A. MACDONALD. 1996. Ploughing behavior of *Babyrousa babyrussa* (Suidae, Mammalia) suggests a scent-marking function. Journal of Zoology (London) 238:209-219.
- MACDONALD, D. W., and R. E. BROWN. 1985. Introduction: the pheromone concept in mammalian chemical communication. Pages 1-18 in R. E. Grown and D. W. Macdonald, editors. Social odours in mammals. Claredon Press, Oxford, U.K.
- MARCHINTON, R. L., and D. H. HIRTH. 1984. Behavior. Pages 129-168 in L. K. Halls, editor. White-tailed deer ecology and management. Stackpole Books, Harrisburg, Pennsylvania., USA.
- \_\_\_\_\_, K. L. JOHANSEN, and K. V. MILLER. 1990. Seasonal variation in marking behavior of white-tailed deer. Pages 295-301 in D. W. Macdonald, D. Müller-Schwarze, and S. E. Natynczuk, editors. Chemical signals in vertebrates. Oxford University Press, Oxford, U.K.
- MASSEI, G., and R. T. BOWYER. 1999. Scent marking in fallow deer: effects of lekking behavior on rubbing and wallowing. Journal of Mammalogy 80:633-638.
- MILLER, K. V., K. E. KAMMERMEYER, R. L. MARCHINTON, and E. B. MOSER. 1987. Population and habitat influences on antler rubbing by white-tailed deer. Journal of Wildlife Management 51:62-66.
- MOEHLMAN, P. D. 1985. The odd-toed ungulates: order Perissodactyla. Pages 531-549 in R. E. Grown and D. W. Macdonald, editors. Social odours in mammals. Claredon Press, Oxford, U.K.
- MÜLLER-SCHWARZE, D. 1972. Social significance of forehead rubbing in black-tailed deer (*Odocoileus hemionus columbianus*). Animal Behaviour 20:788-797.
- OEHLE, M. W., SR., J. A. JENKS, and R. T. BOWYER. 1995. Antler rubs by white-tailed deer: the importance of trees in a prairie environment. Canadian Journal of Zoology 73:1383-1386.
- OWEN-SMITH, R. N. 1971. Territoriality in the white rhinoceros (*Ceratotherium simum*) Burchell. Nature 231:294-296.
- \_\_\_\_\_. 1973. The behavioural ecology of the white rhinoceros. Ph.D. Dissertation, University of Wisconsin, Madison, Wisconsin, USA.
- \_\_\_\_\_. 1975. The social ethology of the white rhinoceros *Ceratotherium simum* (Burchell 1817). Zeitschrift für Tierpsychologie 38:337-384.
- PIENAAR, D. J., A. J. HALL-MARTIN, and P. M. HITCHENS. 1991. Horn growth rates of free-ranging white and black rhinoceros. Koedoe 34:97-105.
- QUAY, W. B., and D. MÜLLER-SCHWARZE. 1970. Functional histology of integumentary glandular regions in black-tailed deer (*Odocoileus hemionus columbianus*). Journal of Mammalogy

- 51:675-694.
- RACHLOW, J. L., and J. BERGER. 1997. Conservation implications of patterns of horn regeneration in dehorned white rhinos. *Conservation Biology* 11:84-91.
- \_\_\_\_\_, and \_\_\_\_\_. 1998. Reproduction and population density: trade-offs for conservation of rhinos *in situ*. *Animal Conservation* 2:37-42.
- \_\_\_\_\_, E. V. BERKELEY, and J. BERGER. 1998. Correlates of male mating strategies in white rhinos (*Ceratotherium simum*). *Journal of Mammalogy* 79:1317-1324.
- \_\_\_\_\_, J. G. KIE, and J. BERGER. 1999. Territoriality and spatial patterns of white rhinoceros in Matobo National Park, Zimbabwe. *African Journal of Ecology* 37:295-304.
- RICE, W. R. 1989. Analyzing tables of statistical tests. *Evolution* 43:223-225.
- RODRIGUEZ, E., and R. WRANGHAM. 1993. Zoopharmacognosy: the use of medicinal plants by animals. Pages 89-105 in H. Stafford and K. Downum, editors. *Recent advances in phytochemistry*. Plenum Press, New York, New York, USA.
- ROSS, M. S. F., and K. R. BRAIN. 1977. *An introduction to phytopharmacy*. Pitman Medical Publishing, Kent, U.K.
- SCHENKEL, R., and L. SCHENKEL-HULLIGER. 1969. Ecology and behaviour of the black rhinoceros (*Diceros bicornis* L.): a field study. Verlag Paul Parey, Hamburg, Germany.
- VOLKMAN, N. J., K. F. ZEMANEK, and D. MÜLLER-SCHWARZ. 1978. Antorbital and forehead secretions of black-tailed deer (*Odocoileus hemionus columbianus*): their role in age-class recognition. *Animal Behaviour* 26:1098-1100.
- WHITTLE, C. L., R. T. BOWYER, T. P. CLAUSEN, and L. K. DUFFY. 2000. Putative pheromones in urine of rutting male moose (*Alces alces*): evolution of an honest advertisement? *Journal of Chemical Ecology* 26:2747-2762.
- ZAR, J. H. 1999. *Biostatistical analysis*. Fourth Edition. Prentice-Hall, Upper Saddle River, New Jersey, USA.