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13 The odd-toed ungulates: order Perrisodactyla

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The order Perrisodactyla is composed of three living families: Tapiridae (tapirs—four species), Rhinocerotidae (rhinos—five species), and Equidae (horses, asses, and zebras—six species) (Table 13.1). This order is a relatively small one today, but included a greater number of species in the geological past (Kingdon 1979). The six living genera each include at least one or more species designated as endangered or vulnerable by the International Union for the Conservation of Nature (IUCN). Perrisodactyls have a non-ruminant digestive system and hence can feed opportunistically on lower-quality forage than ruminant artiodactyls of equivalent body size by eating greater quantities per unit time. However, as an order their reproductive biology is conservative and the resistance of their populations to heavy mortality seems generally to be low.

Tapiridae

Family Tapiridae consists of one genus with four living species: *Tapirus terrestris* (Brazilian tapir); *T. pinchaque* (mountain tapir); *T. bairdii* (Central American tapir); and *T. indicus* (Malayan tapir). Fossils of primitive tapirs (Hydrachyidae) are known from the Eocene and present day forms have retained many primitive characteristics (Colbert 1969). In fact they are often classed as one of the oldest living mammals. Typically both the American and Asiatic species are found in mesic forests and savannas in association with swamps, streams, and/or rivers. All tapir species appear to be primarily browsers and semi-aquatic in their habits. However, due to their low density (most are on the endangered list), densely vegetated habitat, and shy behaviour, few data are available on free-ranging individuals in their natural habitat.

Data are not available on the occurrence of scent glands, or the vomeronasal organ of tapirs. Von Sontag (1974) noted that dark circumorbital spots on *Tapirus terrestris* appeared to be glandular. Adult individuals repeatedly rubbed this region against conspecifics and against urine-marking spots in their compound.

Tapirs appear to be largely asocial, with the only stable group being mother and offspring. Studies in captivity of *T. terrestris* (Hunsaker and Hahn 1965; von Sontag 1974) indicate that the Brazilian tapir may be territorial. Hunsaker and Hahn recorded aggressive behaviour by both males and females when their 'territories' were encroached upon by other tapirs. However, these observations were made on five tapirs enclosed within a 0.2 ha compound where proximity may have prompted aggression. In captivity, Brazilian tapirs regularly urinate, defecate, and bathe (wallow) in artificial pools. Both males and females 'squir-

Table 13.1. Perrisodactyl scent glands and olfactory communication

	Circumorbital	Pedal	Preputial	Circumanal	Circumoral	Perineal	Vomerinasal organ	Flehmen	Dung piles	Dung scraping-pawing	Squirt	Wallow and mud rubbing	Territorial and/or overlapping home range	References
Family Tapiridae	?													
<i>Tapirus terrestris</i> (Brazilian tapir)								+	+		♂,♀	+	T?	1, 2, 5
<i>Tapirus pinchaque</i> (mountain tapir)								+	+		♂,♀	?		3
<i>Tapirus bairdii</i> (Central American tapir)								+	+		♂,♀	+		4
<i>Tapirus indicus</i> (Malayan tapir)								+	+		+	+	OH	2, 5
Family Rhinocerotidae														
<i>Dicerorhinus sumatrensis</i> (Sumatran rhino)								+	+rare	+rare	♂,♀	+	OH	6, 7
<i>Rhinoceros sondaicus</i> (Javan rhino)	+							+	+rare	+rare	♂,♀	+	OH	8
<i>Rhinoceros unicornis</i> (Indian rhino)	+							+	+	+rare	♀,♂	+	T/OH	9
<i>Diceros bicornis</i> (black rhino)								+	+	+	♂,♀	+	T/OH	10-12
<i>Ceratotherium simum</i> (white rhino)		+	+					+	+	+	T♂	+	T	13
Family Equidae														
<i>Equus caballus</i> (horse)				+	+	+	+	+	+	+			T/OH	14-18, 25
<i>Equus burchelli</i> (Burchell's zebra)							+	+	+				OH	19, 25
<i>Equus zebra</i> (mountain zebra)							+	+	+				OH	20, 25
<i>Equus grevyi</i> (Grevy's zebra)							+	+	+				T	21, 25
<i>Equus asinus</i> (African ass)							+	+	+				T/OH	22-25
<i>Equus hemionus</i> (Asian ass)							+	+						25

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5. von Richter (1966).
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10. Goddard (1967).
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12. Frame (1980).
13. Owen-Smith (1973, 1975).
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18. Schaffer (1940).
19. Klingel (1975a).
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23. Moehtman (1974, 1979).
24. Woodward (1979).
25. Estes (1972).

urinate' (a backwards stream or burst of urine), with the adult male most frequently marking particular spots within the compound. Head-rubbing with the putative 'scent gland' was also concentrated on these urination marks. They also concentrate their defecations onto dung piles, and scrape with their hind-legs.

The mountain tapir, *Tapirus pinchaque*, lives at high altitudes (2500–6000 m) and is particularly elusive (Schauenberg 1969). However, limited observations indicate that mountain tapirs also squirt-urinate and defecate on to dung piles. During reproductive behaviour in captivity, males are very aggressive and inflict severe lacerations on the female (Bonney and Crotty 1978). These observations may reinforce the conjecture that tapirs are rather solitary.

Tapirus bairdii, the Central American tapir, has been observed in a small cohesive group on Barro Colorado Island (Terwilliger 1978; Overall 1980). However, these tapirs are provisioned and the grouping pattern may be an artefact of the situation. The Central American tapir often feeds alone, but social interactions were not limited to mother-offspring or reproductive contexts. Tapirs made quiet contact noises and also touched nose to nose. Smell appeared to be important for locating other individuals and the direction of proboscis movement correlated with movements towards conspecifics. *Tapirus bairdii* defecates most frequently in water and spray-urinates.

The Malayan tapir, *Tapirus indicus*, is essentially solitary but is sometimes found in associations of two to three individuals. A radio-collared male tapir had a home range of 12.75 km² that overlapped the home-ranges of several other tapirs in the West Malaysian National Park (Williams and Petrides 1980). Captive studies on the Malayan tapir indicate that their defecation and urination behaviour is similar to that of the rest of the genus, i.e. they use dung piles, squirt-urinate, eliminate in water and/or mud pools, and wallow therein.

The accumulation of odour through urination, defecation, and wallowing may be an important means of leaving a scent trail for a genus in which all species typically inhabit moist and dense vegetation and which generally occur in low numbers. Dung piles and squirt-urination rituals may function as territorial markers or may allow other communication between solitary individuals that have overlapping home-ranges (Eisenberg and Kleiman 1972). All species of *Tapirus* do exhibit flehmen which is commonly accepted to indicate an ability to differentiate between reproductive states on the basis of olfactory information in the urine.

Rhinocerotidae

The family Rhinocerotidae is composed of four genera and five species, all of which are on the endangered list: *Dicerorhinus sumatrensis* (Sumatran rhino), *Rhinoceros sondaicus* (Javan rhino), *Rhinoceros unicornis* (Indian rhino), *Diceros bicornis* (black rhino), and *Ceratotherium simum* (white rhino). Rhinos, like tapirs, are mainly solitary animals. Both the Sumatran and Javan rhino live

in dense forest where visibility is poor. The Sumatran rhino is considered to be the most primitive species belonging to the genus *Dicerorhinus* which is believed to be ancestral to all living Rhinocerotidae (Groves and Kurt 1972). Males are solitary and the only stable group is the mother-offspring unit. Associations of more than two animals are rare (Pollok and Thom 1900; Wroughton and Davidson 1918). Sumatran rhinos are browsers and live in widely overlapping home-ranges (10–30 km²; van Strien 1974; Groves and Kurt 1972). They inhabit hilly forests near water and range from lowland rain-forest to mountain moss-forest (1000–1500 m). Borner (1977) reports localized defecation areas along trails and near streams in his study area. Out of 316 observed dung heaps 17.4 per cent were the defecation of a single animal, 69.4 per cent were the result of 2–4 defecations, and 13.2 per cent were the result of 5+ defecations. Scraping of dung was rare and was associated with only 5 per cent of defecations ($n=316$). The majority (93 per cent) of defecations appeared to involve no more than the individual stopping, defecating, and walking away and piles of dung were rare.

Both male and female Sumatran rhinos may squirt urine, with the spray being directed backwards for up to 6 m. In one sample of 61 urinations, 95 per cent were ritualized urine squirts (Borner 1977). Sumatran rhinos, like tapirs, defecate in water and mud and mud wallow in mud. By wallowing they may be covering their bodies with scent deliberately and subsequently leaving a trail of body marks the vegetation by twisting saplings, beating shrubs, and scraping and scratching trees.

Olfactory communication amongst the Javan rhino (*Rhinoceros sondaicus*) is similar to that of the Sumatran rhino. They are also primarily browsers, living in overlapping home-ranges, in dense lowland rain-forests. In general Javan rhinos are more gregarious than the Sumatran rhinos, but they are nevertheless mainly solitary. They rarely create dung piles or dung scrape but instead probably use pedal scent glands to lay a scent trail. They squirt urine and urinate in their mud wallows. Schenkel and Schenkel-Hulliger (1969a) describe the strong urine smell of rhino wallows, the olfactory impregnation of the rhino's skin, and the transfer of this odour to the soil, vegetation, and air of the 'tunnel-like' paths of a rhino trail.

The Indian rhino (*Rhinoceros unicornis*) inhabits swampy grasslands in India and Nepal. They are predominantly solitary except for mother-offspring groups. Only 9.6 per cent ($n=4352$) of observations involved groups other than solitary individuals or cow-calf pairs (Laurie 1978). Temporary aggregations occur at wallows and feeding grounds. The Indian rhino has been studied by Laurie (1978) who described its social organization and olfactory communication in detail. The Indian rhino displays a particular interest in the urination and defecation sites of other rhino. Laurie describes their ability to use scent to follow and locate each other. Indian rhinos utilize dung piles, defecating onto such sites in 88 per cent of observations ($n=94$). Adult males defecate more frequently than

do females on dung piles. Rhinos normally walk away after defecating and scraping is rare (7 per cent of observations). Like the Javan rhino, the Indian rhino has pedal scent glands. Dung piles were found at the borders of riverine forest and grassland, banks of rivers and wallows, paths and especially path junctions, and near man-made roads and ditches. The frequency of fresh faeces on dung piles positively reflected local variations in rhino density. Laurie checked dung piles for ten consecutive days in December 1973 during which they were used 36 times in total. In the same area, over 10 days in July 1974, 24 sites were used 123 times. Laurie translocated dung from the local population and checked for any difference in the rhinos' response to these. There was no difference in reaction to the local and alien dung.

Laurie (1978) recorded 433 instances of urination by Indian rhinos. Both sexes perform squirt-urination. Males spray backwards 3-4 m on vegetation up to a height of about one metre. Females normally squirt-urinate only during oestrus. The majority of urinations observed were in response to observers (27.7 per cent) and other rhinos or ground scents (26.1 per cent). Adult males urinated four times more frequently than females or subadults ($n=433$). In addition to urinating more frequently overall, adult males usually squirt-urinated ($n=217$, 95 per cent). This ritualized urination was usually accompanied by rubbing the head and horn on vegetation, and foot dragging. This behaviour left broken vegetation, furrows, and vegetation-covered urine. Laurie observed the reactions of rhinos to urine, dung, or tracks of known individuals on 103 occasions, of which 61 per cent involved flehmen. Adult and subadult males performed flehmen significantly more frequently than did females. Adult males reacted to female tracks and urine. Other sex and age classes reacted predominantly to the tracks and urine of adult males. Indian rhinos also performed flehmen near and in mud wallows, where they urinated while wallowing (5.5 per cent of $n=433$). It seems probable that they impregnate their skin with the odour of urine while wallowing, as do tapirs and Sumatran and Javan rhinos.

The home-ranges of adult male Indian rhinos overlap but there is some range exclusivity, and in that sense territorially, between dominant males. Individuals of this species generally occupy overlapping home-ranges within which they move and forage alone. Males often locate females by following their tracks. Thus in a dense habitat in which individuals are widely scattered, Indian rhinos' marking behaviour potentially facilitates the exchange of olfactory information between widely spaced animals.

The black rhino (*Diceros bicornis*) is primarily a browser and lives in a variety of habitats ranging from semidesert to montane forest (Joubert and Eloff 1971; Hitchins 1971; Schenkel and Schenkel-Hulliger 1969b; Frame 1980; Goddard 1966, 1967). However, the black rhino needs to drink regularly and during the dry season stays within 25 km of water. Both species of African rhinos depend on water for temperature control and they will sweat conspicuously (Kingdon 1979) in order to regulate body temperature. They typically live in overlapping

home-ranges although territorial behaviour has been reported by Hitchins (1971) for a population in Zululand. Goddard (1967) found that dung piles were located at random over an individual's home-range. A dung pile might be utilized by several individuals of both sexes but each rhino did not necessarily defecate on every dung pile that it approached. A typical response by a black rhino to a dung pile would be to sniff, wipe with its horn, scrape, defecate, scrape, and walk away. Strange elements in the environment may also elicit defecation behaviour. Goddard investigated aspects of the functional significance of the odours from dung by putting rhino faeces in a net bag and dragging it behind a vehicle in a complicated zig zag trail of up to two miles. Often rhinos followed such trails: (i) 60 per cent followed scent-trails of their own faeces and 50 per cent also defecated on the artificial deposit of their own faeces; (ii) 70 per cent followed scent-trails of dung from animals with which they shared their home-range and 20 per cent also defecated on their home-range companion's dung; and (iii) only 30 per cent followed the scent-trails of dung from animals living several miles distant and also defecated on this artificially laid dung. These interesting data emphasize the importance of scent communication for the 'exchange of information, orienting the movements of individuals, and integrating social and reproductive behavior' (Eisenberg and Kleiman 1972). Black rhino adult males are solitary and the only stable group is mother and offspring. Home-ranges vary in size from 1.33 to 2.6 km². Thus the ability to locate conspecifics through the use of scent-trails may be critical for reproduction. Scent-trails may also enable individuals to avoid one another. In areas of higher density, black rhino in overlapping home-ranges appear to be loosely organized into clans or communities of individuals that are tolerant of each other (Joubert and Eloff 1971; Goddard 1967; Mukinya 1973). Aggregations were temporary but did occur around water and/or wallows. Hitchins (1971), in the one recorded example of territoriality, found three males with subordinate males in their territories (393-465 ha).

Both males and females squirt-urinate. Ritualized urination by females usually occurs when they are in oestrus. Adult males mark bushes, tufts of grass, stumps, and/or stones with 1-4 bursts of urination that spray backwards for distances of 3-4 metres. Head-wiping and horn-beating on bushes sometimes accompanies squirt-urination.

The white rhino (*Ceratotherium simum*) differs from other rhinos and the tapirs in that it is primarily a grazer. In common with the aforementioned perrisodactyls, adult male white rhinos are solitary and the only stable group is mother and offspring. However, white rhinos are most definitely territorial with one dominant territorial male occupying an exclusive home-range of 0.7-2.6 km². The territorial male may tolerate 0-3 subordinate males that occupy the same territory (Owen-Smith 1973).

Owen-Smith (1973, 1975) made a detailed study of the white rhino population in Umfolozi Game Reserve, Zululand. Territorial males performed defeca-

tion and urination rituals that resulted in the placement of persistent scent marks in the environment. Females, subordinate adult males, and subadults had a strictly eliminative manner of urinating and defecating.

Territorial males make kicking movements before and after defecation. In all of 69 observations males sniffed, kicked, defecated, kicked, and walked away. Except for two which were deposited on fresh female dung, defecations by territorial males were on dungheaps. On nine occasions the territorial male rubbed his horn in the dung. This seemed to correlate with the presence of the faeces of a strange male on the dung heap. But when Owen-Smith introduced strange dung experimentally into a territory there was no response. There was an average of 30 dung heaps in each territory, within which they were randomly distributed. Owen-Smith's observations of the communicative function of these dung heaps were that they '(i) provided a record of the visits of many different rhinos; (ii) most of the dung heaps within a territory were marked with the dung of the dominant male; (iii) only territorial bulls kicked and scattered the dung which facilitated a more powerful release of scent, increased the surface area exposed, increased the distribution of the territorial male's scent on the dung heap, and left the scent on the bull's feet and thus a path of scent subsequently'.

Only territorial males squirt-urinated regularly and this display typically consisted of sniffing, horn-wiping (in 50 per cent of cases), scraping, and squirt-urination in 3-5 bursts. Squirt-urination was usually performed at territory boundaries. The rate of squirt-urination in the interior of a territory was 2 per hour, while the rate was 10 per hour along boundaries. A flehmen response was usually given after any class of male smelled a female urination site.

White rhinos have a preputial gland that may contribute a special odour to urine (Cave and Aumonier 1964; Cave 1966; Owen-Smith 1973). Owen-Smith speculated that possible communicative functions of urination by white rhino included '(i) advertisement that the territorial male was in residence and might contribute to maintenance of the status quo and (ii) indication, through hormonal levels, of their social and reproductive status'.

Equidae

The family Equidae is composed of one genus and six species: *Equus asinus* (African ass), *E. hemionus* (Asian ass), *E. grevyi* (Grevy's zebra), *E. zebra* (mountain zebra), *E. quagga* (common zebra), and *E. caballus* (horse). These species live in a variety of habitats ranging from desert (asses) to tropical grasslands (zebras) to temperate grasslands (horses). Early equids were forest dwellers and may have been similar to tapirs in their solitary habits (Kingdon 1979). Present-day species exhibit social behaviour ranging from that typical of species in arid environments involving male territory, with the only stable group being that of mother and offspring, to the system more characteristic of mesic habitats,

which involves stable unimale or multimale harem groups (Klingel 1975a, Moehlman 1974). These two types of social behaviour appear to be the extremes of a continuum of social organization ranging from a system in which territoriality plays an important role and social bonding is limited to the more socially organized and cohesive family groups. Generally, the territorial type of social organization has been described for *Equus asinus* and *E. grevyi*, with the stable family group being typical of *E. quagga*, *E. zebra*, and *E. caballus*. However, field research on various populations of feral asses (Moehlman 1979; McCort 1980) and feral horses (Rubenstein 1978) has revealed intraspecific behavioural plasticity and variability of social organization.

Equus grevyi lives in arid grasslands and characteristically has a social organization in which there are territorial males and the only stable bonds are between female and offspring (Klingel 1969a, 1975a). Their territories (~10 km²) are the largest recorded for herbivores and conspecifics of all age and sex classes are tolerated. However, only the territorial male has access to oestrous females. Territorial males have large dung piles along the boundaries of their areas and these may serve as fixed orientation points for the resident (Klingel 1975b). Dung piles are also found near paths, waterholes, and rivers and may be the result of more than one individual's activity (Kingdon 1979).

Equus asinus (African ass) has endangered status in its native habitat, Ethiopia. Limited observations by Klingel (1977) indicate that in this arid district (Danakil Desert) the species is territorial and only mother and offspring form stable groups. Thriving populations of feral asses have been studied in North America (Moehlman 1974, 1979; Woodward 1979). Feral asses in Death Valley National Monument (Moehlman 1974) were browsers and displayed social organization typical of equids in an arid habitat, i.e. 10 per cent of adult males held territories adjacent to the major water source, and female and offspring formed the only permanent groups. Males were often solitary (23.9 per cent of $n=1158$ observations) and the general population trend was that of small groups of two to four individuals (57.8 per cent of $n=1158$). Non-territorial individuals live in overlapping home-ranges of up to 103.6 km². Large aggregations (8-21) occurred rarely (3.3 per cent of $n=1158$) and were associated with scarce resources, i.e. water and/or oestrous females.

Territorial asses (Moehlman 1974) form dung piles along boundaries and within their territories. Dung piles also occur along trails and in the vicinity of watering areas. These dung piles are not limited to the use of any one animal and all males freely defecated on them. Females of all age classes showed little interest in dung and simply defecated where they stood and walked away (Table 13.2). Adult males often defecated in single deposits ($n=42$). On 38 per cent of these occasions they smelled their defecation, pawed it, flehmened, and/or urinated on it. Adult males also smelled and defecated on dung piles ($n=87$). In 54 per cent of the observations the male simply smelled the dung pile and walked away. The typical display in the remaining observations consisted of

group excreta was urination (92 per cent of $n=76$ responses). Females were never observed to respond to excreta.

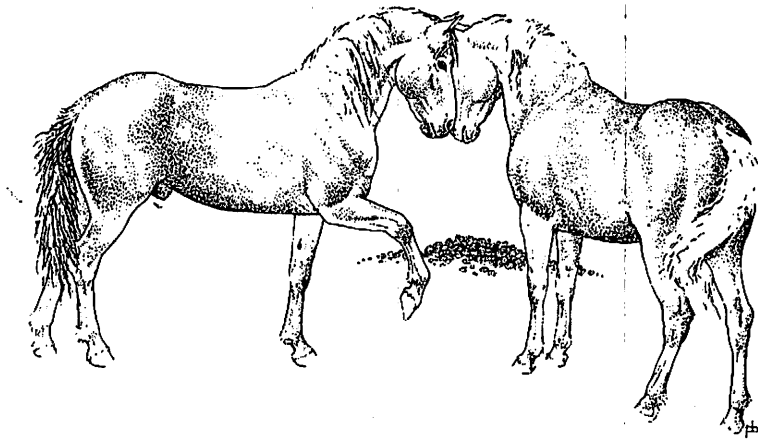


Fig. 13.2. Mustang stallions sniffing nostrils at a dung pile.

Order of elimination among males was correlated with dominance, with subordinate male eliminations being covered by that of the dominant male. Most interactions between males involved defecation, usually at dung piles ($n=186$ defecations by stallions with 89.8 per cent at dung piles). Utilization of dung piles was an adult male prerogative. Typical behaviour involved smelling, pawing, defecating, and occasionally urinating. Aggressive encounters between rival males were often associated with dung piles. When two groups met the two dominant males might approach each other, smell the dung pile together, both defecate on it (in turn or simultaneously), smell the pile, and then fight or separate. In the Pryor Mountain study area most dung piles were found on or near trails or in proximity to water holes, i.e. highly frequented sites. Feist and McCullough postulated that for this non-territorial population dung piles and urination sites had visual and olfactory importance in terms of dominance relationships, associations, and information on hormonal state which persisted over time. Miller and Denniston (1979) observed interband dominance hierarchy in a population of horses studied in the Red Desert of Wyoming. Dung piles might serve also as communication posts between such components of a population.

Flehmen occurred most frequently during the early part of the breeding season. Most observations involved a male response to female genitalia, urine, or faeces (53 per cent of $n=55$), but males also flehmened in response to their own urine.

In the same study area, Turner, Kirkpatrick, and Perkins (1981) also quantified eliminative behaviour in stallions. They defined eliminative behaviour as the behavioural response of stallions to urination and/or defecation by other horses which was simultaneously noticeable by the stallion. Elimination behaviour as such was not performed by females or immature animals. The response of stallions to adult female elimination varied seasonally. The average frequency of response ($n=172$) was 43.4 per cent. However, frequency of response peaked in the breeding season (May—93 per cent; June—89 per cent) and was very low in November—February (1 per cent). The average number of eliminations per hour did not differ between months. The seasonality of stallion eliminative behaviour correlated positively and strongly with the breeding season and seasonal increase in stallion plasma androgens and mare plasma steroids. Stallions, under laboratory conditions, have responded appropriately to oestrous behaviour by mares that have been ovariectomized. Thus sex steroids from adrenal sources may mediate oestrous behaviour in female horses (Asa, Goldfoot, Garcia, and Ginther 1980).

Rubenstein's (1978) study of territorial harem groups on Shackleford Banks indicates that eliminative behaviour in that locale is similar to that of non-territorial horses but that spatial placement of dung piles is different. Large dung piles occur both on territory boundaries and within territories. Encounters between rival males involve the same ritualized sequence of defecations, dung-sniffing, and aggression as described by Feist and McCullough (1975).

Discussion

Perrisodactyls emerged in the Palaeocene and radiated in the Eocene and Oligocene. During the latter period they were abundant in America and Eurasia. Competitive pressure from artiodactyls which possess an efficient foregut digestive system may have led to the reduction or removal of perrisodactyls from many herbivore niches (Kingdon 1979). The remaining species appear to have either (i) specialized in high-fibre diets or (ii) evolved large body size as a strategy to avoid ruminant competition (Janis 1976). Janis postulates that perrisodactyls became cellulose eaters and caecal fermenters during the Palaeocene when their body size was relatively small. Perrisodactyls, unlike ruminants, are not limited by rumen size and passage rates, and hence can process more herbage and survive on a poorer quality (higher fibre) diet.

Primitive perrisodactyls were probably small forest-dwelling herbivores (Colbert 1969). Today the tapirs are considered to be the most primitive members of the order. In fact they are considered little changed from the Eocene fossils. They are typically solitary, live in overlapping home-ranges, and feed on browse. Eisenberg and Lockhart (1972) have suggested that the tendency of forest ungulates to be solitary may be partly due to the effect of poor visibility upon group communication and coordination. Perhaps a more

critical factor is the spatial and temporal availability of food. In dense forest, food is more widely scattered and not quickly renewable, hence predisposing tapirs to be widely distributed (Jarman 1974; Laurie 1978). In any case, tapirs appear to be highly dependent on scent marks for locating conspecifics. Anatomically they have very large skeletal nasal openings (Willoughby 1974) and their long proboscis is flexible and sensitive. Although they do not appear to have scent glands they do scrape their dung and also wallow in mud in which they have defecated and urinated. These excretory odours probably leave scent-trails as individuals move through the dense vegetation.

The most 'primitive' rhino, the Sumatran rhino, also lives in dense tropical forests. Similar to tapirs they are primarily solitary, live in overlapping home-ranges, and are browsers. Squirt-urination and wallowing in mud-defecation sites are their major modes of scent communication. Javan and Indian rhino both have pedal scent glands which may be important for leaving scent trails. Indian rhino males are territorial and dung-piles are a common phenomenon. Javan and Indian rhinos are found in more open forests and alluvial floodplains and compared with Sumatran rhinos are more commonly found in aggregations of two or more. Black rhino are primarily browsers and are found in more open habitat. Depending on their density they may have a spacing system of overlapping home-ranges or what appear to be territories inhabited by males in a dominance hierarchy. Black rhinos of both sexes squirt-urinate, utilize dung piles, and dung scrape. The latter behaviour appears to enable individuals to discriminate between scents of conspecifics and to track their dung trails appropriately. Among white rhinos some major departures from the general perrisodactyl condition occur. The white rhino has a high genetic variability (blood protein) and may be in an active stage of evolution (Osterhoff and Keep 1970, in Kingdon 1979), possibly because its adaptation to a diet of grass may be relatively recent. In any case they live in an open habitat, have a relatively evenly distributed and abundant food supply, eat grass, and males live in territories. Creating dung piles and scraping and squirting urine are the prerogatives of the dominant and breeding territorial male only. Females and subordinate males do not engage in this type of display. For rhinos, scent remains a major mode of communication and perhaps a prime regulator of their social existence (Kingdon 1979).

Equids are capable of great plasticity in their social behaviour and mating systems. Their social organization ranges from stable harem bands in mesic habitats where grazing is the main mode of feeding, to territorial males and small stable groups of mother and offspring in more arid habitat, where browse is the predominant food source. Dung piling and pawing is commonplace, and in territorial populations dung heaps may be localized along boundaries. Responses to dung and urination are made primarily by dominant males. Rival males may engage in defecation rituals associated with aggressive displays. Dominant males will typically cover female excreta and hence potentially announce their presence

and mask the female's scent. Hormonal levels in the urine corresponding to ovulation may provide important cues to a female's reproductive status. However, adrenal steroids may play an equally important role. Ovariectomized and seasonally anoestrous horses display oestrous behaviour. 'Sexual activity outside the breeding season, made possible by the absence of complete control of steroids from the ovaries over oestrous behaviour, could contribute to the maintenance of social bonds between the harem stallion and his mares' (Asa *et al.* 1980).

Among perrisodactyls dung piles, scent trails (due to dung scraping or pedal scent glands), and urine marks (on the ground or sprayed on to vegetation) provide important olfactory information on location, social, and reproductive status for mobile members of, often low-density, populations.

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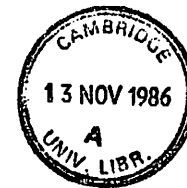
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