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Equus zebra.

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Equus zebra Linnaeus, 1758

Mountain Zebra

Equus zebra Linnaeus, 1758:74. Type locality suggested by Roberts (1951:244) as Paardeberg, near Malmesbury, southwestern Cape Province, Republic of South Africa.

Equus montanus Burchell, 1822:139. No locality given, but mentions Paardeberg.

Hippotigris campestris Gray, 1852:277. Type locality "mountains of South Africa."

Equus indica Trouessart, 1898:797. Type locality not given.

Equus hartmannae Matschie, 1898:17. Type locality between Hoanib and Unilab rivers, 19°S, 13°E, Koakoland, northern Namibia.

Equus penricei Thomas, 1900:465. Type locality Providencia, Moninho Valley, 70 km northeast of Mossamedes, southwestern Angola.

Equus wardi Ridgeway, 1910:799. Believed to be a menagerie hybrid between *E. zebra* and *E. burchelli chapmani*.

CONTEXT AND CONTENT. Order Perissodactyla, Family Equidae, Genus *Equus*, in which six to nine Recent species are recognized (Grubb, 1981). Two subspecies of *E. zebra* were recognized by Meester et al. (1986), who also listed the synonymy quoted here.

E. z. hartmannae Matschie, 1898:17, see above (*matschiei* Zukowsky, 1924, and *penricei* Thomas are synonyms). Colloquial names are Hartmann zebra or Hartmann's mountain zebra; Hartmannse or Damaralandse bergkwagga (Afrikaans); Ongórlo-hambar úndu (Herero); and Nu!khrob or Nu!go:reb (Nama Hottentot).

E. z. zebra Linnaeus, 1758:74, see above (*montanus* Burchell, *campestris* Gray, *indica* Trouessart and *frederici* Trouessart, 1905, are synonyms). Colloquial names are Cape mountain zebra; Kaapse bergkwagga (Afrikaans); Daou or Dauw (Cape Hottentot); iDauwa (Xhosa).

DIAGNOSIS. *Equus zebra* is a medium-sized, striped equid. It differs from *E. burchelli* in that the dark stripes on the head and body are narrower and consequently more numerous. There is a marked contrast between their width and that of the dark stripes on the hindquarters (Fig. 1), that are clearly much broader and show no sign of "shadow" stripes between them, a characteristic of southern *E. burchelli* subspecies (Smithers, 1983). *E. zebra* has white underparts, with a narrow dark central line extending over the chest and belly; in *E. burchelli*, the dark body stripes often extend to the ventral midline. *E. zebra* has a distinct dewlap, unique among equids. In *E. zebra*, narrow dark markings form a "gridiron" pattern over the sacral area between the uppermost horizontal dark stripes of the hindquarters (Fig. 2; Smithers, 1983).

GENERAL CHARACTERS. Adult *E. z. zebra* have a shoulder height of 116 to 128 cm; mares have a mass of ca. 234 kg (range, 204 to 257 kg, including two emaciated specimens), whereas the mass of a stallion was estimated at 250 to 260 kg (Smithers, 1983). Adult mares of *E. z. hartmannae* average 276 kg and stallions 298 kg, with stallions older than 7 years averaging 343 kg (Joubert, 1974*a*). These stallions had a mean shoulder height of 144.5 cm.

Equus zebra has a short erect mane (Fig. 1). The hair of the middorsal region grows forwards from a whorl on the rump (Smithers, 1983). The hair is 10.0 ± 1.8 mm long, oval or oblong in cross-section with a densely black medulla and clear cortex with a pigmented spot; the cuticular scale pattern is an irregular waved mosaic along the entire length (Buys and Keogh, 1984). No two individuals have identical stripe patterns, nor are the two sides of the body mirror images of each other (Penzhorn, 1979). The ground color is white, with black to deep chocolate-brown stripes, whose depth of color may be a factor of the molt (Smithers, 1983). Stripes on the head are narrowest, followed by those on the body and on the neck; horizontal to oblique stripes on the hindquarters are clearly much broader (Fig. 1). The legs are distinctly striped to the hooves, the stripes on the hind legs being broader than those on the front legs. Dark vertical body stripes discontinue abruptly on the lower part of the flanks; underparts are white, with a narrow central dark stripe extending over the chest and belly (Smithers, 1983). In some populations of *E. z. zebra*, the cranial 2 to 3 dark vertical stripes behind the shoulders tend to continue ventrally, even joining the central longitudinal dark stripe (Lloyd, 1984). The upper 2 to 3 dark stripes on the hindquarters are exceptionally broad in *E. z. zebra*, less so in *E. z. hartmannae*, where some white stripes may be broader than the black ones (Smithers, 1983).

The narrow dark markings of the "gridiron" pattern on the rump (Fig. 2) are continued onto the tail and extend to the whisk of long black or blackish-brown hair toward the tip, the hair dangling to the level of the hock (Smithers, 1983).

Bard (1977) postulated that a single mechanism capable of generating the stripe pattern exists in zebra species; it operates at different times in the embryonic development of different species. Geometric analysis showed that this period was during the fourth week in *E. zebra*.

The dark and light stripes of *E. z. hartmannae* are about equal in width, especially on the hindquarters, but in some individuals the light stripes are wider. Dust-rolling tends to obscure the light color of the coat, tinging it various shades of red (Smithers, 1983).

The tip of the muzzle is black, and immediately behind the mouth and below the eyes the stripes are suffused chestnut to orange-colored (Smithers, 1983). The ears of mountain zebras are rounded and 21 to 23 cm long, 18 to 22% of the withers height (Groves and Willoughby, 1981). When viewed from the front, ears have white tips and black margins, while on the backs they are white at the bases, then black with white tips (Smithers, 1983). Mountain

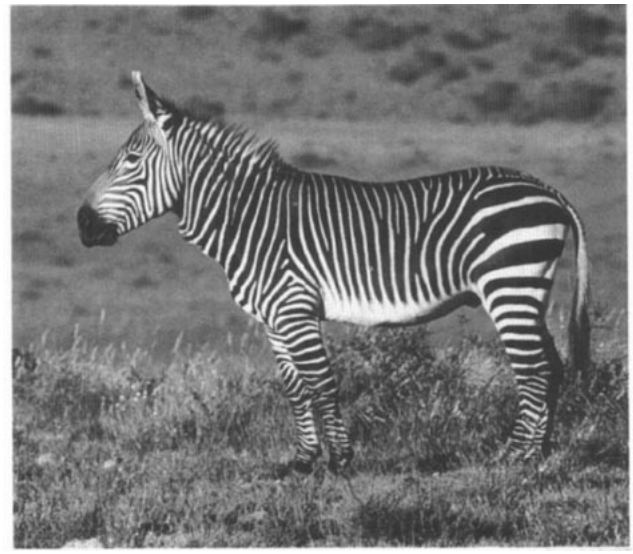

FIG. 1. An adult Cape mountain zebra stallion, *Equus zebra zebra*, from the Mountain Zebra National Park, Cape Province, Republic of South Africa. Note dewlap, unmarked belly, absence of "shadow stripes" between the broad dark stripes on the hindquarters, and stripes on the legs that extend to the hooves. (Photograph by B. L. Penzhorn.)

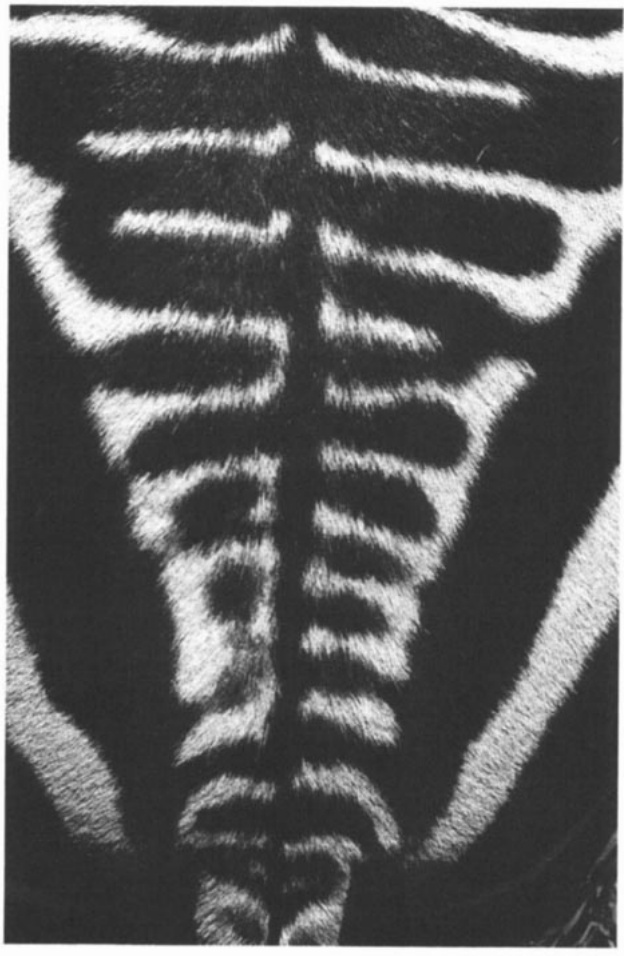

FIG. 2. The "gridiron" pattern on the rump of a Cape mountain zebra, *Equus zebra zebra*. (Photograph by A. O. Zaayman, National Parks Board of South Africa.)

zebra hooves are compact with hard ventral surfaces, presumably an adaptation to the type of terrain inhabited (Smithers, 1983). The chestnuts, confined to the forelimbs, are large in mountain zebras (about 76 by 51 mm; Groves and Willoughby, 1981).

The skulls of *Equus* sp. superficially resemble one another, but there are considerable differences among taxa (Eisenmann and de Giuli, 1974; Groves and Willoughby, 1981). Some characteristic features of *E. zebra* skulls are (Fig. 3): orbit somewhat behind the posterior border of M3; dorsoventral diameter of orbit greater than in *E. burchelli*, giving a rounder orbit; external auditory meatus large (3% of basal length of skull), and directed horizontally and somewhat rostrally; maxillary tuberosity not extending as far back as in *E. burchelli*, so that the pterygopalatine fossa is visible from below. The nasofrontal suture is nearly straight, and the temporal lines diverge more rapidly rostrally than in *E. burchelli*, and at a wider angle.

In postcranial skeletal morphology mountain zebras show considerable similarity to assess, *E. asinus* (Groves and Willoughby, 1981): scapula and metapodials short; ungual phalanges short on both fore and hind limbs; as in all zebras, metatarsus longer than metacarpus; ratio between plantar length of ungual phalanx to its anterior length lowest in mountain (and Burchell's) zebras.

DISTRIBUTION. Historically *E. z. zebra* occurred throughout the mountainous regions of the Cape Province of South Africa from the Amatola Mountains in the Cathcart District westward and northward to the Kamiesberg in Namaqualand (Millar, 1970). Today natural populations occur in the Mountain Zebra National Park (MZNP; 32°15′S, 25°41′E), Gamka Mountain Reserve (33°42′S, 21°54′E), in the Kamanassie Mountains, and possibly in the Kouga and Baviaanskloof mountains of the southern Cape. Populations originating mostly from the MZNP have been established in Karoo

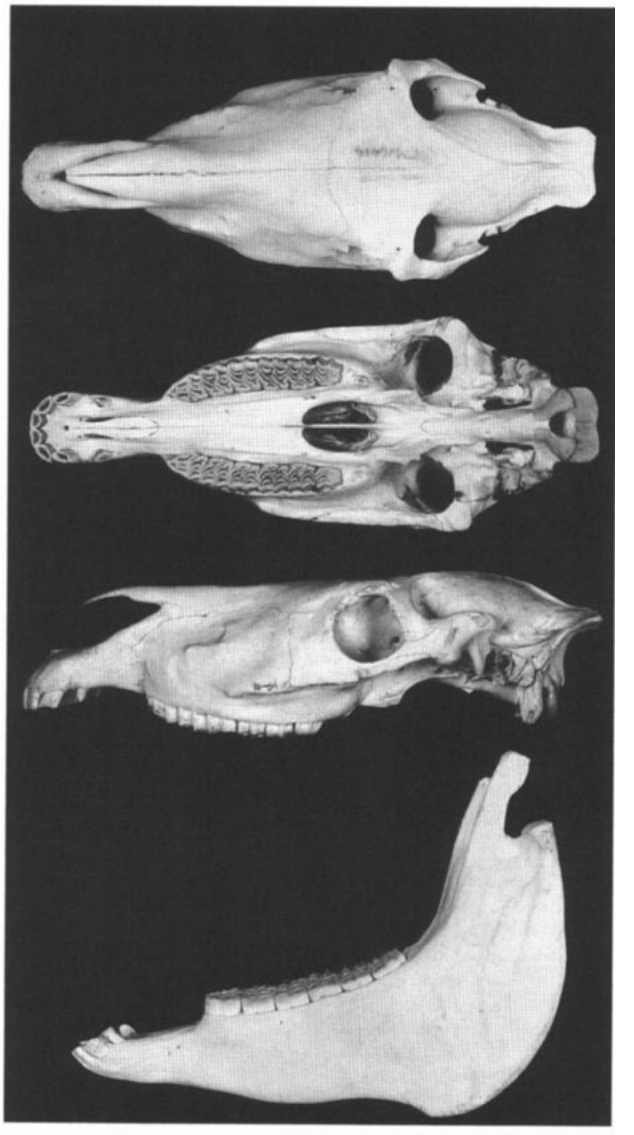

FIG. 3. Dorsal, ventral, and lateral views of cranium, and lateral view of lower jaw of a male *Equus zebra*, Transvaal Museum 16414. (Photographs by H. Smit.)

National Park (32°17′S, 26°30′E), Karoo Nature Reserve (32°14′S, 24°31′E), Commando Drift Nature Reserve (32°06′S, 26°03′E), De Hoop Nature Reserve (DHNR; 34°26′S, 20°30′E), and Tsolwana Game Ranch, Ciskei (Fig. 4; Lloyd, 1984).

In Namibia (South West Africa), *E. z. hartmannae* occur in the mountainous transition zone between the Namib Desert in the west and the plateau in the east, with a marginal extension into the extreme southwest of Angola (Iona National Park; Smithers, 1983). Their distribution today is discontinuous (Fig. 4); in the north they occur in Kaokoland and in Damaraland southwards to about the Ugab River and eastwards to farms in the Outjo District. South of this, they occur in the Erongo Mountains in southeastern Damaraland on the borders of the Omaruru and Karibib districts, and much more extensively southward on the escarpment from the Swakop River south to the Naukluft Mountains and eastward along the Kuiseb and Gaub drainage into the Khomas Hochland. Southward there is a break in their distribution and they reoccur in the Fish River Canyon and Huns Mountains near the Orange River (Joubert, 1973).

FOSSIL RECORD. *Equus zebra* is rather sparsely recognized as a fossil (Churcher and Richardson, 1978). In the southwestern Cape Province of South Africa, *E. zebra* was recorded together with the extinct *E. capensis* in late Pleistocene and Holocene assemblages (Hendey, 1974*a*, 1974*b*). A fossil skull found near

Norval's Pont on the upper Orange River, Cape Province, was described as *E. z. greatheadi* (Lundholm, 1952).

FORM AND FUNCTION. Mountain zebras resemble other equids in their anatomy and physiology, with some minor differences. Digestive efficiency of *E. z. hartmannae* does not differ significantly from that of the domestic horse (Joubert and Louw, 1977). The maximum urine osmolality of 1465 mOsm and the mean plasma: urine concentration (n = 8) of 4.1 indicate a moderate urine concentrating ability; behavioral thermoregulation (that is, shade-seeking) appears to be an adaptive trait to minimize evaporative water loss (Joubert, 1972*a*; Joubert and Louw, 1977).

Blood chemical parameters, as well as erythrocyte and leukocyte values, of *E. zebra* are generally in agreement with those of domestic horses (van Heerden et al., 1985; Young, 1966). Serum potassium concentrations of shot *E. z. zebra* (n = 8) obtained within 3 to 20 min after death ranged from 4.6 to 6.7 m mol/l ($\bar{X}$ = 5.5) and serum sodium concentrations ranged from 137 to 149 m mol/l ($\bar{X}$ = 141; van Heerden and Dauth, 1985). Serum potassium concentrations are slightly higher than recorded for domestic horses and *E. burchelli*. It was impossible to determine whether this was related to the method of culling, technique of collection, a physiologic characteristic of the species, or simply as a result of an immediate and progressive postmortem increase in serum potassium concentration. In the MZNP, *E. z. zebra* of all ages frequent mineral licks, especially during summer. Calcium was the only mineral with higher concentrations at licks than in all surrounding soil samples (Penzhorn, 1982*a*). Hofmeyr et al. (1973) claimed that blood samples collected from *E. z. hartmannae* (n = 8) revealed that those subjected to greatest stress before being shot showed a tendency towards elevated plasma creatine kinase and lactate levels, and an increased haematocrit, but actual figures were not given.

The "milk" dental formula (primary dentition) is i3/3, c1/1, p4/4, total 32; the permanent or adult dental formula (secondary dentition) is i3/3, c1/1, p3/3, m3/3, total 40. The rudimentary first milk premolar is not replaced by a permanent premolar. The milk canine in both sexes and the permanent canine, when present in the mare, are significantly smaller than the permanent canine of the stallion (Joubert, 1972*b*; Penzhorn, 1982*b*).

Mountain zebras injected with a combination of etorphine hydrochloride, azaperone, and hyoscine hydrobromide were all immobile within 3 to 5 min and recumbent within 5 to 9 min (Young and Penzhorn, 1972).

Distinct seasonal quantitative differences in chemical composition of *E. z. zebra* feces seemed to reflect differences in the type of forage available or eaten, and could possibly be used as an indicator of veld quality (Erasmus et al., 1978).

ONTOGENY AND REPRODUCTION. Foals are born year-around, with a peak in summer (Joubert, 1974*b*; Penzhorn, 1985). In a winter-rainfall area (DHNR) most foals are born in spring or early summer (Penzhorn and Lloyd, 1987). In a semi-arid summer-rainfall area (MZNP) conception occurs later in the season when the spring is dry (Penzhorn, 1985).

Testes of *E. z. hartmannae* reach their maximum size at about 42 months ($\bar{X}$ = 87.6 g; n = 24). The mean mass declined slightly from a maximum of 99.4 g in January (the southern hemisphere summer) to a minimum of 83.1 g in September. Sperm abnormalities averaged 9% throughout the year (Joubert, 1974*b*). Generally, colts do not succeed in becoming herd stallions before they are 5 years old (Penzhorn, 1984*b*). In MZNP, spermatogenesis was absent in bachelor colts 24, 29, and 48 months old, but was starting in a 54-month-old bachelor. A DHNR colt running with mares in the absence of adult stallions sired a foal when 42 months old (Penzhorn and Lloyd, 1987).

A gestation period of 364 days has been recorded (Joubert, 1974*b*). First recorded conception by a MZNP filly was at 26 months, and mean age at first foaling was 66.5 months in MZNP (range, 38 to 105; n = 29; Penzhorn, 1985) and 53.4 months in DHNR (range, 46 to 58; n = 5; Penzhorn and Lloyd, 1987). Two MZNP mares were recorded to foal for the last time when >21 years old (Penzhorn, 1985). A foaling interval of 375 days has been observed in a captive mare (Penzhorn, 1975). She conceived during postpartum estrus. A median foaling interval of 25 months (range, 13 to 69) was found in 49 MZNP mares, some foaling up to six times during the study period. There were no significant differences in foaling intervals of mares older and younger than 13 years

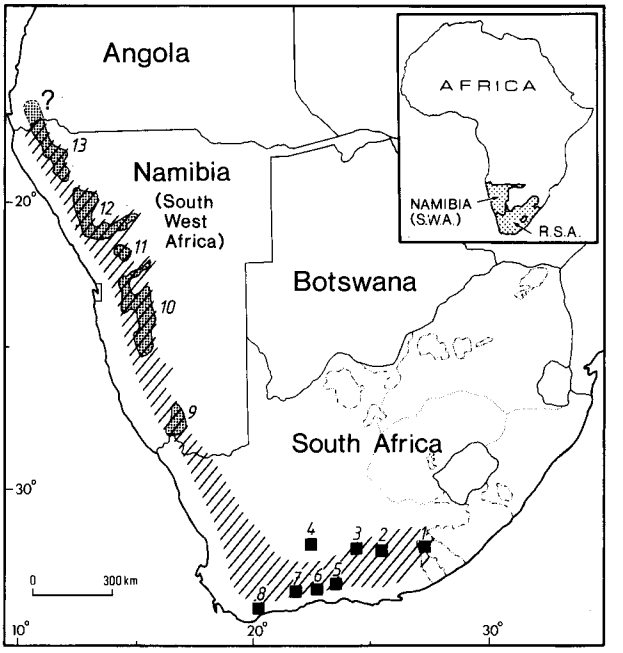

FIG. 4. Map showing the present discontinuous distribution of Cape mountain zebras *Equus zebra zebra* in the Republic of South Africa and Hartmann zebra *E. z. hartmannae* in Namibia (South West Africa), as well as their presumed historic ranges: 1, Tsolwana Game Ranch, Ciskei; 2, Mountain Zebra National Park; 3, Karoo Nature Reserve; 4, Karoo National Park; 5, Kouga/Baviaanskloof Mountains; 6, Kamanassie Mountains; 7, Gamka Mountain Reserve; 8, De Hoop Nature Reserve; 9, Fish River Canyon and Huns Mountains; 10, Swakop River south to Naukluft Mountains, including Khomas Hochland; 11, Erongo Mountains; 12, Damaraland and Outjo District; 13, Kaokoland). (Map drawn by I. Cornelius after du Plessis (1969), Joubert (1973), Penzhorn (1975), and Shortridge (1934).

(Penzhorn, 1985). Average mass of paired ovaries from breeding *E. z. hartmannae* mares was 47.3 g (range, 19.6 to 141.5 g; n = 26; Joubert, 1974*b*). The incidence of dystocias in *E. z. zebra* was <1% (Penzhorn, 1984*a*).

During its first few weeks of life a mountain zebra foal remains close to its dam; the dam actively prevents contact between the foal and other members of the herd by threatening any individual that approaches too closely, irrespective of rank (Joubert, 1972*c*; Penzhorn, 1984*b*). The duration of lactation varies; time of final weaning seems to depend mainly on the imminent birth of a sibling. Suckling intention is signalled to the dam by the foal pressing its body against her chest as it moves around her to attempt to suckle on the other side (Joubert, 1972*c*). The total suckling time usually ranges from 90 s to 2 min, and usually consists of a long initial suckling period lasting ca. 1 min followed by a resting period of a few seconds during which the foal raises its head. A second, shorter suckling period of 10 to 20 s usually completes the bout (Penzhorn, 1984*b*). Foals usually suckle at about hourly intervals during the day until ca. 3 months old when suckling frequency decreases. From the 10th month onward only 1 to 3 suckling bouts/day were recorded. Infrequent suckling was recorded in foals up to 20 months old. Foals start to nibble at grass when only a few days old (Penzhorn, 1984*b*).

Lloyd and Harper (1980) reported a primiparous *E. z. zebra* mare rejecting her new-born foal to appropriate a 4-week-old foal of another mare in the same breeding herd. Penzhorn (1984*b*) recorded the adoption of a ca. 10-week-old filly of a primiparous mare by a mare that was nursing her own 2-month-old filly. The adopted filly remained with her foster mother for ca. 8 months before disappearing.

At birth, *E. z. hartmannae* foals have a mass of 25 kg (n = 5) and a head and body length of 120 cm. Stallions require 7 years to attain maximum mass (Joubert, 1974*a*).

Tooth eruption order, replacement sequence, and tooth wear pattern resemble that of other equids, but infundibula last longer in

premaxillary incisors of *E. z. zebra* than in other taxa, apparently due to a slower rate of wear (Joubert, 1972*b*; Penzhorn, 1982*b*, 1987; Penzhorn and Grimbeek, 1987). Annual laminae in the cementum of incisors can be used to estimate age (Penzhorn, 1982*b*).

ECOLOGY. Mountain zebras are not territorial, but breeding herds inhabit home ranges, with extensive overlap. In MZNP the mean minimum home range (Hayne, 1949; Mohr, 1947) of *E. z. zebra* breeding herds was 9.4 km² (range, 3.1 to 16.0 km², n = 16; Penzhorn, 1982*c*). *E. z. hartmannae* breeding herds have winter grazing areas of 6 to 10 km² in Daan Viljoen Game Reserve and 10 to 20 km² in the Otjovasandu area of Etosha National Park; summer grazing areas are considerably smaller at both localities; at Otjovasandu, winter and summer grazing areas are separated by ca. 120 km (Joubert, 1972*c*). When two breeding herds of *E. z. zebra* split, home ranges of the resulting herds included those of the original herds, but were larger (Penzhorn, 1982*c*). This illustrates the role of mares in delimiting group activities hence defining the home range of a breeding herd.

Breeding herds of *E. z. zebra* in the MZNP show seasonal differences in selection of certain vegetational communities. Selection may not be primarily for forage, but also for shelter, drinking places, and mineral licks, but the rainfall pattern also influences distribution of zebras (Penzhorn, 1982*d*).

In MZNP, Grobler (1983) found that *E. z. zebra* fed on only 26% of plants available at feeding sites and only seven of 17 grass species present. Selection was directed at the greener plant species with a high leaf:stalk ratio and little or no moribund material. Nevertheless, they still were coarse grazers and used both stem and leaf components of selected grasses. They fed at 40 to 80 mm above the ground, except when eating seed heads of certain grass species. Protein levels of grasses eaten exceeded 4%. *Themeda triandra* was the principal food for the zebra. Other heavily used species (some of them seasonal) were *Cymbopogon plurinodis*, *Heteropogon contortus*, *Setaria neglecta*, and *Enneapogon scoparius*. *Digitaria eriantha* was eaten occasionally and *Eragrostis curvula* was used significantly only during early winter when seed heads were eaten. MZNP zebras also were observed to eat grasses: *Aristida congesta*, *Cynodon incompletus*, *Eragrostis chloromelas*, *E. lehmanniana*, *Merxmuellera disticha*, and *Tragus berteronianus*, and woody plants: *Pentzia incana*, *Eriocephalus ericoides*, *Lycium* sp., and *Acacia karroo*, were recorded to feed on inflorescences of Restionaceae in DHNR (Penzhorn, 1982*d*).

Late winter is a critical period for survival of *E. z. zebra* in MZNP. In addition to both the deteriorating quality of the forage as the dry season progresses and the cold winter weather, the zebras also carry large tick burdens (Horak et al., 1986; Penzhorn, 1984*a*). *Gasterophilus intestinalis*, *G. nasalis*, and *G. pecorum* are bot-flies recovered from *E. z. zebra* in MZNP. The following ixodid ticks have been recovered: *Amblyomma hebraeum*, *Hyalomma marginatum rufipes*, *H. truncatum*, *Ixodes* sp., *Margaropus winthemi*, *Rhipicephalus arnoldi*, *Rhipicephalus* sp. (near *R. capensis*), *R. evertsi evertsi*, and *R. glabroscutatum*. In Namibia, *E. z. hartmannae* were found to harbor the bot-flies *Gasterophilus meridionalis*, *G. nasalis*, *G. pecorum*, *Rhinoestrus usbekistanicus*, and the ixodid ticks *Hyalomma marginatum rufipes*, *H. truncatum*, and *Rhipicephalus evertsi mimeticus* (Horak et al., 1984). The following nematodes were recovered from *E. z. hartmannae* in Namibia: *Craterostomum acuticaudatum*, *Crossocephalus vivíparus*, *Cyathostomum alveatum*, *C. montgomeryi*, *C. tetracanthum*, *Cylicocyclus adersi*, *C. auriculatus*, *C. triramosus*, *Cylicodontophorus reineckei*, *C. schuermanni*, *Cylicostephanus bidentatus*, *C. calicatus*, *C. longiconus*, *C. minutus*, *Cylindropharynx* sp., *Draschia megastoma*, *Habronema longistoma*, *H. malani*, *H. majus*, *H. muscae*, *H. zebrae*, *Oxyuris equi*, *Probstmayria vivipara*, *Setaria equina*, *Strongylus equinus*, *Triodontophorus hartmannae*, and *T. serratus* (Scialdo-Krecek, 1983, 1984; Scialdo-Krecek and Malan, 1984; Scialdo-Krecek et al., 1983). Other nematodes reported from mountain zebras, often from zoo animals, are: *Cyathostomum coronatum*, *Cylicocyclus insigne*, *Cylicostomum calicatum*, *C. longibursatum*, *Cylindropharynx brevicauda*, *C. intermedia*, *C. longicauda*, *Dictyocaulus arnfieldi*, *Parascaris equorum*, *Poteriostomum imparidentatum*, *Strongylus asini*, *S. vulgaris*, *Triodontophorus minor*, and *T. tenuicollis* (Round, 1968). The cestodes *Anaplocephala magna* and *A. perfoliata* were recovered from *E. z. zebra* in MZNP, as was the haemoprotozoan *Babesia equi* (Penzhorn, 1984*a*; Young et al., 1973). A *Sarcocystis* sp., with domestic dogs as final hosts, has been recovered from *E. z. hartmannae* (Markus et al., 1983).

Dental abnormalities were found in seven of 37 *E. z. zebra* skulls (Penzhorn, 1984*c*). Intraventricular thrombosis was found in two *E. z. zebra*, while *Actinobacillus equuli* was cultured from kidneys and liver of a 3-month-old filly and from various organs of a 20-year-old mare (Bath, 1975, 1979).

In Namibia, *E. z. hartmannae* are subject to predation by lions (*Panthera leo*), leopards (*P. pardus*), cheetahs (*Acinonyx jubatus*), spotted hyaenas (*Crocuta crocuta*), and hunting dogs (*Lycaon pictus*; Joubert, 1974*c*). In one instance, it appeared from spoor and other signs that a stallion had not only kicked an adult spotted hyaena to death, but had continued to press home its attack over a distance of 100 m, repeatedly kicking the dead hyaena (Smithers, 1983). Along the Kuiseb Canyon in the central Namib Desert, significantly more *E. z. hartmannae* mares than stallions are taken by spotted hyaenas, the only large predators in the area (Tilson et al., 1980).

BEHAVIOR. Mountain zebra populations consist of breeding herds (one adult stallion, one to five mares, and their foals); and bachelor groups (Joubert, 1972*c*; Klingel, 1968, 1969; Penzhorn, 1979, 1984*b*). The largest herd of *E. z. zebra* encountered in MZNP consisted of 13 individuals (1:5:7y), but the mean herd size was 4.7 (n = 21) with 2.4 mares/herd, similar to that among *E. z. hartmannae* (Joubert, 1972*c*; Penzhorn, 1984*b*). Breeding herds remain stable over many years. One MZNP stallion stayed with the same mares for >10 years, until he was 17 years old (Penzhorn, 1984*b*). Mares usually remain in breeding herds for life.

If a herd stallion is displaced, the herd is taken over as a unit by a stallion, although sometimes the herd may split (Joubert, 1972*c*; Penzhorn, 1984*b*). Attempts at stallion displacement usually lead to serious fighting, involving biting and kicking; severe wounds often are inflicted (Penzhorn, 1984*b*). Breeding herds are formed initially when a bachelor stallion acquires a mare, usually a young one that recently left her maternal herd or, rarely, an adult mare from a fragmented herd. Bachelors <5 years old usually lack the strength or stamina to become herd stallions (Joubert, 1972*c*; Penzhorn, 1984*b*).

Equus z. zebra fillies and colts leave their maternal herds of their own accord and are not forced out by the herd stallion. The herd stallion actively tries herding them back (Penzhorn, 1984*b*). *E. z. hartmannae* mares vigorously try to expel their 14 to 16-month-old foals from the herd before birth of a sibling (Joubert, 1972*c*). In the MZNP, *E. z. zebra* colts and fillies leave their maternal herds at a mean age of ca. 22 months (range, 13 to 37; n = 27). Birth of a sibling does not seem to be most influential in this regard, as foals may leave the herd even when no sibling is born. Foals average leaving the herd ca. 3 months (range, 0 to 14) after the birth of a sibling. A 37-month-old colt was still with his maternal herd 20 months after the birth of a sibling (Penzhorn, 1984*b*). Most foals leave their maternal herds in summer. Sexual activity increases in summer, possibly stimulating exodus, but birth of a sibling or lack of playmates also may be contributory; factors responsible for dispersal of young are not yet understood. Colts roam singly or in unstable groups loosely associated with bachelor groups. Older fillies are taken up into existing breeding herds or are herded by bachelors within a few weeks or months. Younger fillies remain solitary or with bachelor groups much longer before being herded. Colts and fillies rejoin their maternal herds for short periods after varying intervals (Penzhorn, 1984*b*).

Social hierarchies exist in breeding herds, with the stallion being dominant (Joubert, 1972*c*; Penzhorn, 1984*b*). A linear hierarchy is evident among mares of small herds, but in larger (probably the longest-established) herds, each individual apparently knows its relative position and social hierarchies are difficult to determine. In the long-established herd the role of the stallion is relatively passive, but with the establishment of a new herd, the stallion must actively herd mares and foals to prevent them from leaving, especially recently acquired mares. In *E. z. zebra*, estrus and birth of a foal can change the social hierarchy, with the mare temporarily rising in status, but reproductive success is not a requisite for social dominance (Penzhorn, 1984*b*).

There is no clear-cut correlation between dominance and leadership in mountain zebras, although dominant mares tend to initiate

most activities in some herds. The stallion usually leads when a breeding herd approaches a drinking site. When mountain zebras move from danger, a mare, usually the one with the youngest foal, takes the lead while the stallion lags behind, frequently wheeling around (Joubert, 1972*c*; Penzhorn, 1984*b*).

The neonatal sex ratio of 1:1 (Joubert, 1974*c*; Penzhorn, 1975) and polygynous social organization of mountain zebras result in surplus stallions, that are accommodated in bachelor groups and compose 17 to 20% of the total population. Bachelor groups form the reservoir from which herd stallions are recruited. The structure of bachelor groups is much less rigid than that of breeding herds. There are no well-defined herds, but small core groups that remain fairly stable over long periods are joined by other individuals from time to time (Penzhorn, 1984*b*). Core group members usually are older bachelors and often have family ties. Bachelor groups often attach to a breeding herd and remain with the herd for varying lengths of time. It seems likely that at least one bachelor originated in that herd (Penzhorn, 1984*b*).

Threat behavior takes the form of pulling back the ears against the head, lowering the head, with neck outstretched and teeth bared, tail lashing, and finally a rush towards the antagonist (Joubert, 1972*c*; Penzhorn, 1984*b*). Moving away is an adequate response to threat, but may be accompanied by a kick in defense. Fighting, although rarely observed, consists of biting at the opponent's head, neck, rump, and legs, and kicking at the opponent with either front or hind legs (Penzhorn, 1984*b*).

Play rarely is recorded in *E. z. zebra*, but is more frequent in *E. z. hartmannae* (Joubert, 1972*c*; Penzhorn, 1984*b*). Racing or chasing is the first play pattern to appear. Challenge games consist of nasonasal contact followed by mutual body rubbing or grooming. Challenge games of foals usually develop into chasing, but in bachelors they develop mostly into play-fighting. Play-fighting contains all elements of serious fighting, but the movements are exaggerated.

Vocalization includes a high-pitched alarm call from the stallion when danger threatens and a drawn-out squeal uttered by a bachelor when confronted by the herd stallion. The herd stallion also may utter an alarm snort. This is actuated, on sensing danger, by an audible intake of air through the nose, a sharp expelling of air, followed by an audible intake. A soft sign of contentment when feeding caused by air forced between closed lips, is audible over short distances only (Joubert, 1972*c*; Penzhorn, 1984*b*).

When two breeding herds come into proximity, the herd stallions approach each other and perform a challenge ritual, consisting of nasonasal contact, body rubbing, and nasogenital contact; then both stallions resume grazing and gradually move back to their respective herds (Joubert, 1972*c*; Penzhorn, 1984*b*). Challenge between a herd stallion and a bachelor usually consists of a brief nasonasal contact only. The final approach is made by the bachelor in a submissive posture (head lowered, grimace, squeal); he makes chewing motions, possibly grooming-intention movements or a displacement activity derived from nursing behavior (Crowell-Davis et al., 1985; Feist and McCullough, 1976; Tyler, 1972; Zeeb, 1959). Challenge between herd stallion and bachelor occasionally develops into mutual grooming (Penzhorn, 1984*b*).

Mountain zebras react to flight or alarm signals of black wildebeest (*Connochaetes gnou*) but they seldom react to similar signals of smaller species of antelope such as springbok (*Antidorcas marsupialis*) or blesbok (*Damaliscus dorcas phillipsi*). Unlike *E. burchelli*, *E. z. zebra* do not appear to associate with antelope (Penzhorn, 1984*b*). Palewinged starlings (*Onychognathus nabouroup*), and rarely redwinged starlings (*O. morio*) and forktailed drongos (*Dicrurus adsimilis*) associate with mountain zebras, presumably to remove external parasites from them (Joubert, 1972*c*; Penzhorn, 1981).

Grazing and resting occupy most of the daylight hours. There are generally three main grazing periods during the day: a few hours after dawn, late morning, and from mid-afternoon to dusk. A grazing mountain zebra moves slowly foward, raises its head after each few mouthfuls, and stands chewing momentarily before resuming grazing (Joubert, 1972*a*; Penzhorn, 1984*b*). Resting bouts with the zebras standing or lying down (sternal or lateral recumbency) usually occur during mid-morning and early afternoon. Foals spend longer periods resting than adults. *E. z. zebra* in MZNP do not actively seek shady resting sites whereas this behavior is pronounced among *E. z. hartmannae* (Blaine, 1922; Joubert, 1972*a*; Penzhorn, 1984*b*). *E. z. zebra* in MZNP drink daily, mainly during the second and third grazing periods, while *E. z. hartmannae* in Namibia drink at 0700 to 0900 h and at 1900 to 2200 h. They avoid muddy water around the edge of a dam; they usually wade a few paces into the water before drinking (Joubert 1972*a*; Penzhorn, 1984*b*).

During cold weather, mountain zebras seek shelter in wooded ravines and shallow caves (Penzhorn, 1984*b*). They often graze in the lee of a hill or ridge, protected from the wind. On cold mornings they frequent east-facing slopes to sun themselves (Joubert, 1972*a*).

Grooming patterns are essentially similar in all equids (Klingel, 1972; Trumler, 1959). Mutual grooming has a utilitarian function as areas that the animal cannot groom itself are groomed by other members of the group, but it also has attained a secondary function in maintenance of group cohesion. The most frequent mutual grooming in *E. z. zebra* breeding herds is between mares and their foals, but foal-mare (not dam), foal-herd stallion, mare-herd stallion, and mare-mare grooming also occurs (Penzhorn, 1984*b*). Mother-foal grooming usually is elicited by the foal. Individual grooming consists of localized muscle contractions, shaking, striking one part of the body against another or against the ground, rubbing, scratching, nibbling, and dust-bathing (Joubert, 1972*a*; Penzhorn, 1984*b*). *E. z. zebra* usually dust-bathe at least once daily and frequently more often (Penzhorn, 1984*b*).

GENETICS. The diploid chromosome number of mountain zebras is 32, the lowest of the Equidae, with a fundamental number of 60 (Heinichen, 1967, 1970). There are 13 pairs of meta-submetacentric, 1 pair of subtelocentric, and 1 pair of acrocentric autosomes; the X and Y chromosomes are both submetacentric. A free-living mare running with a feral donkey *E. asinus* stallion gave birth to a hybrid foal (Penzhorn, 1985). Hybrids between *E. zebra* and *E. caballus*, *E. asinus*, *E. hemionus* and *E. burchelli* have been reported (Gray, 1972).

REMARKS. Although formerly widespread in the Cape Province, *E. z. zebra* probably were never numerous. The first protection measure was enacted in 1742, when hunting of this species was prohibited (van der Merwe, 1962). Nevertheless, *E. z. zebra* were extensively hunted for their hides, because they competed with livestock for grazing, and because they alledgedly broke fences (Penzhorn, 1975). By the early 1930s it was evident that *E. z. zebra* soon would become extinct if not specially protected. In 1937, the 1,712-ha Babylons Toren farm near Cradock, eastern Cape Province, was purchased and proclaimed the Mountain Zebra National Park. The population consisted of five stallions and one mare (Pringle, 1982). In 1950, when the population had dwindled to two stallions, a neighboring farmer donated his five stallions and six mares to the MZNP (Bigalke, 1952). By 1964, the population had reached 25. In that year a number of adjoining farms where some zebras occurred were incorporated into the MZNP, increasing the area to 6536 ha and the population to 55 (Penzhorn, 1975).

The MZNP population presently is maintained at ca. 220, and as many as 40 zebras are removed annually for re-establishment of breeding nuclei elsewhere within their original range. In all, 280 *E. z. zebra* have been distributed from the MZNP (Lloyd, 1984). At present the Karoo National Park has a population of ca. 85, Karoo Nature Reserve 35, De Hoop Nature Reserve 30, Tsolwana Game Ranch 28, Gamka Mountain Reserve 21, and the Kammanassie Mountains ca. 12. The total population of *E. z. zebra* was ca. 474 in August 1985 (Smithers, 1986). In the first South African Red Data Book, *E. z. zebra* was designated "Endangered" (Skinner et al., 1977). Within a decade the position had improved markedly, and in the revised edition they could be removed from that category and placed in the lower category "Vulnerable" (Smithers, 1986).

Based on an aerial census conducted in 1968, the total number of *E. z. hartmannae* in Namibia was ca. 7,000 (Joubert, 1973). Later estimates increased this to 11,000 (Joubert and Mostert, 1975; Joubert et al., 1983) and 13,000 (Joubert, in litt.).

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