

Chapter 302

Zebra Reproduction

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Introduction

Few studies have investigated the reproductive biology of wild equids; much of what we know about zebra species has come from dissections following culling.¹⁻³ Zoo research has proven useful in determining additional details regarding the ovulatory cycling of females,⁴ and the timing of puberty and breeding life in both males and females. Behavioral studies both in the field and in captivity have helped to clarify these factors.⁵⁻⁸ In addition, behavioral studies have revealed how breeding behavior, the degree of breeding seasonality, stages of parturition, mother-infant behavior, and the dispersal of young males and females can vary in the different species.^{9,10} Using this combination of behavioral, physiological, and demographic data, we explain the reproductive biology of each age and sex class of plains zebra (*Equus burchelli*), the two subspecies of mountain zebra – Cape mountain zebra (*Equus zebra zebra*) and Hartmann's zebra (*Equus zebra hartmannae*) – and Grevy's zebra (*Equus grevyi*), and relate its relevance to their ecology and natural history.

Social context: mating patterns and their ecological determinants

Zebras live in two broadly different types of societies.¹¹⁻¹³ In one, typified by plains and mountain zebras, females and males live in unimale-multifemale family groups with their infants, yearlings, and two-year-olds. These so-called 'harem' groups are relatively stable with males and females living together for many years.¹⁴ In the other, typified by Grevy's zebras, female associations are short-lived and females often roam in groups without males. Fusing and fissioning of individuals creates these open membership groups that wander through territories of isolated males. From the perspective of males, both systems are polygynous since reproductively active

and dominant males often mate with more than one female. In plains zebras, polygyny involves harem defense since females form strong associations, while in Grevy's zebras it involves resource defense as males defend grazing areas that females seek. As in any polygynous system, younger, less dominant males form bachelor groups and attempt to cuckold stallions while strengthening ties to females. From the perspective of females, however, these mating systems offer different reproductive opportunities. In plains zebras, females are monoandrous since all females in a harem bond to a particular male. In Grevy's zebras, females are polyandrous since they often move across territorial boundaries and mate with a variety of males in succession.

Each mating system emerges as a response to particular ecological circumstances.¹² In general, zebra males provide important material rewards to females that increase their reproductive success. By increasing vigilance and enabling females to move unhindered when seeking resources, some males enable females to spend more time grazing.¹² Females associating with the most dominant males, or those rising rapidly in rank, rear the most offspring to the age of independence.¹³ But this only applies in mesic habitats where food and water – the two key resources females need to sustain themselves and their young – are located close enough to each other so that females of different reproductive states can stay together and simultaneously derive these time-related benefits that males provide. For Grevy's zebras inhabiting more arid areas where rainfall is highly unpredictable, food and water are typically far apart, thus females having different needs cannot stay together and the social fabric becomes torn. As a result, female associations are weak. Since females exhibiting either postpartum or cycling estrus are equally valuable to males, those of high rank defend territories along routes to water so that they can mate with lactating females residing near water and

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non-lactating females that must come to drink every 3–5 days.^{15,16} Males of lesser rank defend territories in grazing areas and thus gain access to a more limited pool of reproductively active females.

It is within these social and ecological contexts that the reproductive biology of zebras must be examined. Only by appreciating how socioecological selective pressures shape social relationships and mating behavior can the similarities and differences in reproduction exhibited by the various age and sex classes of each zebra species be understood.

Mare

Behavior

Female-female bonds in all zebra species are weak. There is little competition over food and cooperative interactions in terms of allogrooming or mutual defense of young are rare. Similarly, there is minimal competition for mates, but female mountain zebras compete for dominance, and rank affects reproductive fitness. Although both dominant and subordinate females produce approximately the same number of offspring over a lifetime, the survival of young born to high-ranking females exceeds that of young born to low-ranking females.¹⁷ In addition, as daughters take on the rank of their mothers, dominant females will produce disproportionately more female offspring. Bonds between mothers and their young weaken as offspring mature, with both males and fe-

males leaving their natal groups by 3 years of age. Reproducing females and males interact regularly. Females generally initiate movements, with males directing the group from the side or the rear. Lactating females often initiate moves to water and lead the way.¹⁸

Mating often involves conflict among the sexes. Females typically adopt a rigid position with tail raised when initiating copulation. More often, however, the male identifies females in heat by sniffing or licking the genital region. Resting his head on a female's rump or biting at the withers often precedes mounting by the male. If a female is not ready to mate she either walks out from under the male or uses her hind legs to drive him away.

Seasonality

Plains zebra

In general, zebra are less seasonal than other African species. Plains zebra foals are born throughout the year, although peaks do exist during the long rains (Figure 302.1). Klingel⁶ reported that 85.5% of foals were born from October to March in the Ngorongoro Crater, Tanzania. Similarly, Smuts² found that 82.6% of foals were born between September and April in Kruger National Park, South Africa. Since the gestation period is about 12 months, mating activity must occur throughout the year with a peak during the summer months. Plains zebra in North American and

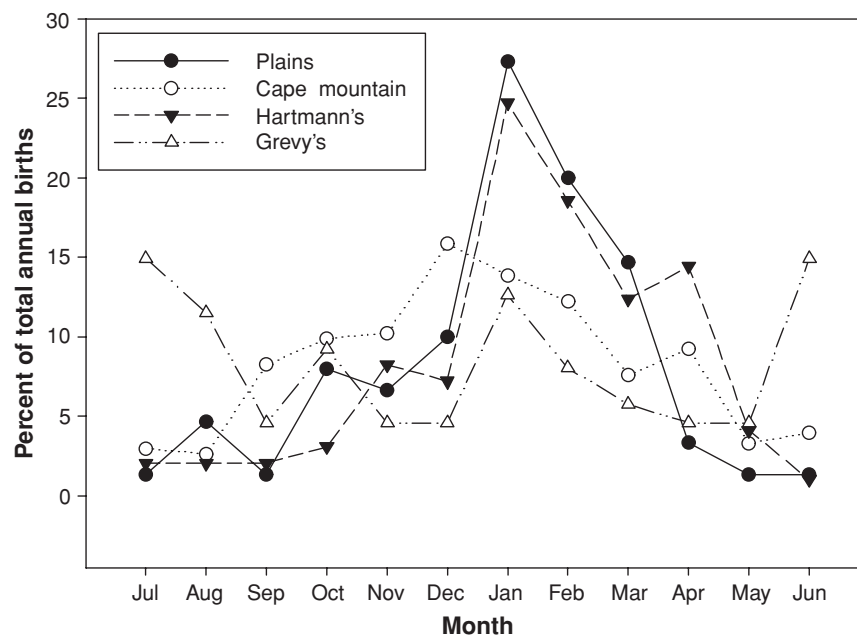


Figure 302.1 Seasonal distribution of births for the different zebra species. Data compiled and adapted from Klingel²⁶ (plains zebra), Joubert²¹ (Cape mountain zebra), Westlin-van Aarde *et al.*²² (Hartmann's zebra), and Dobroruka *et al.*⁵ (Grevy's zebra). Grevy's data are from captive animals.

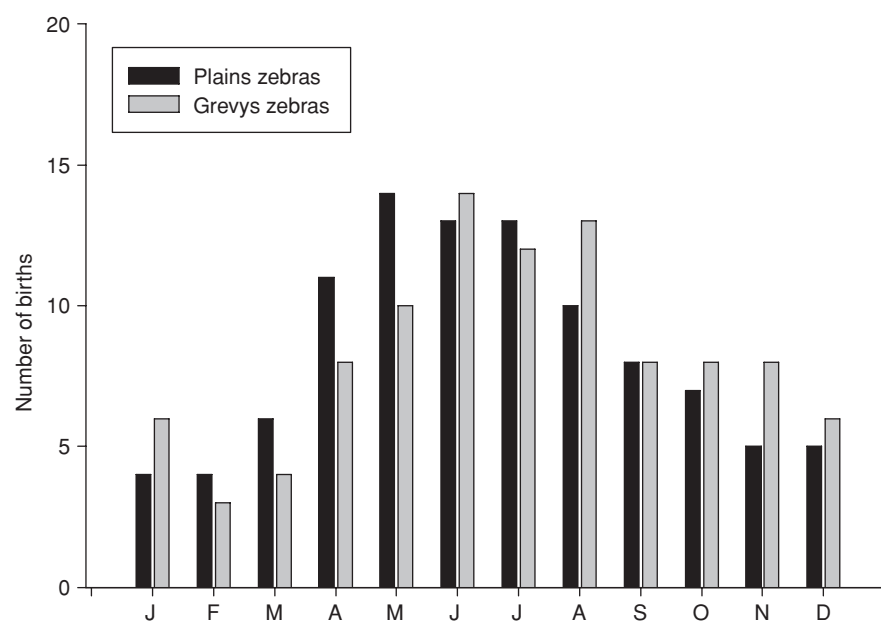


Figure 302.2 Seasonal distribution of births for plains zebra and Grevy's zebra held in zoos; data are taken from the Plains Zebra Regional Studbook for North American zoos¹⁹ and the Grevy's Zebra International Studbook.²⁵

European zoos¹⁹ have given birth in every month of the year, but births cluster in spring and summer (Figure 302.2). However, trends for spring and summer births in zoos are sometimes the result of management decisions for young to be born in those months.

Mountain zebra

Free-ranging Cape mountain zebra mares in the Mountain Zebra National Park and De Hoop Nature Reserve, South Africa,²⁰ foal year round with peaks around the rains. Over 68% of Cape mountain foals are born during the rains, from November through April.⁷ Free-ranging Hartmann's zebra in southwest Africa are similar, with 81–86% of foaling occurring from November through April.^{21,22} During a 3-year study of Hartmann's zebra, mating activity was only seen from September to April, with a peak in February.²¹ These data, coupled with the fact that the gestation period is about 1 year, indicate that mating during the rest of the year is quite rare.

Grevy's zebra

Grevy's zebra are perhaps the most seasonal of the zebras with peaks of mating occurring during the long rains in July and August, and the short rains in October and November.²³ In the free-ranging populations of northern Kenya, breeding is highly dependent upon available resources, with peaks in estrus coinciding with higher resource availability.²⁴ Con-

versely, mares can be induced into anestrus when resources are scarce.¹⁵ Gestation is a bit longer in Grevy's zebra (about 390 days), so peaks of mating activity must occur in June through July and September through October. Captive animals in Dvur Kralove Zoo in the former Czechoslovakia gave birth every month from 1973 to 1985, although peaks did exist in January and from June through August,⁵ generally following the foaling schedule of wild populations (see Figure 302.1). Data from the Grevy's Zebra International Studbook²⁵ for the period 1984 through 2004 show a similar trend, with births throughout the year but concentrated more in spring and summer months. As with plains zebra, this trend may reflect management strategies, but year-round endocrine monitoring of the herd of Grevy's zebra at the Saint Louis Zoo (J.E. Bauman, C.S. Asa, and M. Fischer, unpublished) has revealed a pattern of lower concentrations of progesterone following ovulations in winter, suggesting that fertility might indeed be lower during that period.

Puberty and breeding life

Plains zebra

Early work on plains zebra defined puberty in mares as the onset of first estrus and estrus behaviors.^{1,2,6} King reported first estrus to occur at an average age of 2 years 4 months, ranging from 1 year 8 months to 2 years 9 months. Klingel²⁶ found that Ngorongoro mares exhibited first estrus earlier, at 13–15 months of age. Similarly, Smuts² found that the first estrus of

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Table 302.1 Reproductive data for plains and Grevy's zebras held in zoos

	Plains zebra ^a	Grevy's zebra ^b
<i>Females</i>		
Number of females	334	169
Youngest to give birth ^c	1 year 8 months	2 years 6 months
Oldest to give birth	26 years 1 month	28 years 4 months
Most offspring	15 foals	13 foals
<i>Males</i>		
Number of males	149	85
Youngest to sire offspring	7 months	1 year 11 months
Oldest to sire offspring ^d	26 years 9 months	25 years 9 months

^aData taken from the *Plains Zebra North American Regional Studbook* (2004)¹⁸ for records from 1980 through 2003.

^bData taken from the *Grevy's Zebra International Studbook* (2004)²⁴ for records from 1984 through 2004.

^cAge at parturition.

^dAge when female conceived.

mares in Kruger National Park occurs at 1.5 to 2 years of age. The Plains Zebra North American Regional Studbook (Table 302.1)¹⁹ has parturition records for females at 1 year and 8 months, 1 year and 10 months, and 1 year and 11 months of age; the data represent the female's age at the time she gave birth, not the time she conceived.

Klingel⁶ estimated the reproductive potential of mares as one foal per year from the age of 3.5 to about 15 to 18 years. They observed 120 mares for three seasons. Fifteen percent of the animals had three foals (one per year), 33% had two, 42% had one, and 10% had no offspring. On average, mares had a surviving foal once every 2 years. This coincides with data from a captive animal at Chester Zoo, England, that at 17 years old, was still breeding after having produced six foals since attaining sexual maturity.⁶ North American Regional Studbook (Table 302.1)¹⁹ records show that 10 females over 20 years of age produced foals, the oldest at 26 years. Twelve females gave birth to more than 10 foals over a lifetime. Of 1232 recorded births, 11 (1%) were twins.

Mountain zebra

In Mountain Zebra National Park, young Cape mountain zebra mares leave their natal herds at a mean age of 1 year 10 months; often they are in first estrus at this time.⁷ Lloyd and Rasa¹⁷ reported Cape mountain fillies in De Hoop Nature Reserve leaving a bit earlier, at a mean age of 1 year 7 months (again during first estrus). First foaling has been recorded at ages as young as 2 years¹⁷ to as old as 5 years 7 months.⁷ Regardless of the exact age at first foaling, it seems likely that the mares do not become sexually mature until several months after first estrus. The ac-

tual age of first estrus in Hartmann's zebra has not been recorded, but free-ranging mares have their first foal at about 2 years of age. Young mares are expelled from the natal group at 14 to 16 months of age,²⁷ at which time they may be experiencing first estrus.

The reproductive potential of Cape mountain zebra mares has been estimated at about one foal every 25 months, with a range of 13–69 months.^{7,20} Similarly, Lloyd and Rasa¹⁷ calculated an average interbirth interval of 27.4 months. Given a reproductive lifespan of about 15 years, a Cape mountain zebra mare can be expected to produce eight to nine foals in her lifetime. The reproductive potential of Hartmann's zebra has not been reported explicitly, but may be surmised by maternal behavior. Hartmann's zebra mares wean their foals at approximately 10 months of age, and begin to actively expel the foals at 13 to 16 months of age, shortly before the birth of their next foal. Given this behavior, we can expect the reproductive potential of Hartmann's zebra mares to be about one foal every 1 to 1.5 years.

Grevy's zebra

Puberty in free-ranging Grevy's zebra mares has been estimated to occur at 3 to 4 years of age¹ with mating occurring during the second estrus and conception occurring after two or three estrus cycles. However, captive animals have been reported to reach puberty and achieve conception at much younger ages. The International Studbook has records of one female at 2 years 6 months and another at 2 years 10 months giving birth for the first time (Table 302.1).²⁵ In a study at the Saint Louis Zoo that monitored behavior and fecal hormones,⁴ a 2-year-old female conceived but aborted an 18-cm fetus at about day 100 of gestation. She subsequently mated and aborted at least one more time before successfully carrying a foal to term, which was born when she was 3 years 4 months of age. Managers had suspected that young females were more likely to experience abortions, and the results of this study supported that hypothesis. This suggests that females may be able to ovulate and conceive before their reproductive tracts are sufficiently mature to maintain pregnancy. Age at puberty is affected by nutrition, but may also be influenced by social constraints in the wild that may not be present in captivity.⁴

Free-ranging Grevy's zebra mares may breed from 1 to a few months after foaling, with an average reproductive potential of one foal every 2 years.^{1,23} In captive animals, the mean interbirth interval has been estimated at 18 months (range 14.2–34.8 months⁵) and 19.75 months (range 13–27 months⁸) in Czechoslovakian and North American zoos, respectively. However, management strategies likely bias

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the average intervals. According to the International Studbook (Table 302.1),²⁵ the oldest female to give birth was 28 years of age, with 10 females over the age of 20 giving birth. Over a lifetime, there were seven females that each produced more than 10 foals, one of which gave birth to 13.

The female reproductive organs

Plains zebra

The female reproductive organs of culled animals were studied in detail by King.¹ The plains zebra mare has two ovaries, each about 5 cm in length. The ovaries connect to the fallopian tubes (oviducts), which conduct the ovum from the ovary to the uterus. Each oviduct attaches to one of the two horns of the uterus, which are approximately 15 cm in length. The horns attach to the body of the uterus (10–15 cm long). Caudal to the uterus is the cervix, about 5 cm long, which enters the vagina. The vagina is about 15–20 cm long, and is quite elastic, allowing it to expand. The external opening of the vagina lies ventral to the rectum. The mare has two mammary glands, which are smaller in virgin mares. They have two ducts each, which open externally.

Mountain zebra

Detailed dissections of the female reproductive organs have not been reported in the mountain zebra species. Given their average mass of 234 kg and 276 kg for Cape mountain and Hartmann's zebra mares, respectively,²⁸ they are likely to have organs intermediate in size and shape to those of plains and Grevy's zebra. For example, Westlin van-Aarde *et al.*²² reported that the ovaries of Hartmann's zebra females are heavier than those of plains zebra² at every stage of the reproductive cycle.

Grevy's zebra

The reproductive organs of the Grevy's zebra mare are similar, but are about 10% larger than those of plains zebra.¹

Estrus and ovulation

Smuts divided the estrus cycle in all zebra species into five phases: proestrus, estrus, metestrus, diestrus, and anestrus.² Proestrus is the phase immediately preceding estrus, and is characterized by an increase in ovarian activity. Mares during this phase will generally refuse a stallion's attempts to mount. Estrus is the period of acceptance of the male, when a mare will exhibit the display posture and 'stand'

for a stallion. A mare in the display posture stands with her legs slightly apart and her tail lifted. The posture is quite conspicuous, even from a distance, and seems to be an important attractant for the stallion.⁶ Increased interest of the stallion, the open-mouthed facial expression of the mare (often called 'jawing'), and mating are other diagnostic features of estrus.¹ During metestrus reproductive activity subsides as the diestrus phase begins. Diestrus is the period of luteal activity between ovulatory cycles, and anestrus is the period of sexual rest during the non-breeding season. For the most part, a mare in anestrus does not ovulate, and the uterus is small and anemic.²⁹ This is the normal state of the filly before puberty.

In zebra mares, ovulation occurs at the ovarian fossa, a depression at the free, ventral edge of the ovary.² This structure, present in all equid species, is lined with germinal cells destined to develop into ova.³⁰ Ovulation occurs only at this structure and never from any other region on the ovary.³¹ In plains zebras (and probably mountain zebras), the ovarian fossa is not present at puberty, but develops after a few estrus cycles. In Grevy's zebra, the ovarian fossa is fully developed at puberty, but in other respects resembles that of the other zebra species.

Ovarian activity during the estrus cycle

Plains zebra

Ovarian activity during the estrus cycle was outlined by Smuts² using data collected from 310 free-ranging mares shot during a game cropping campaign in the Kruger National Park, South Africa. During proestrus, there is an increase in the follicular activity, with one follicle generally larger than the others. As in horses, regressing corpora lutea from previous cycles may be present. The estrus phase is similar to proestrus except that the follicle that is going to rupture is clearly identified and the mare now accepts the stallion. In metestrus, the Graafian follicle has ruptured, a corpus hemorrhagicum forms, and the follicular cavity fills with a lymph-like fluid. As the cells lining the ruptured follicle undergo rapid division and become luteinized, a corpus luteum is formed. The corpus luteum attains its maximum size during this period, after which it gradually regresses. Follicular activity is largely dormant. Should the mare fail to conceive, she enters diestrus or anestrus. During diestrus, a new wave of follicles starts developing and the corpus luteum starts to regress. Diestrus is generally followed by the proestrus phase. The corpus luteum is still present by the time the succeeding cycle commences, and in this respect, the plains zebra mare is similar to the

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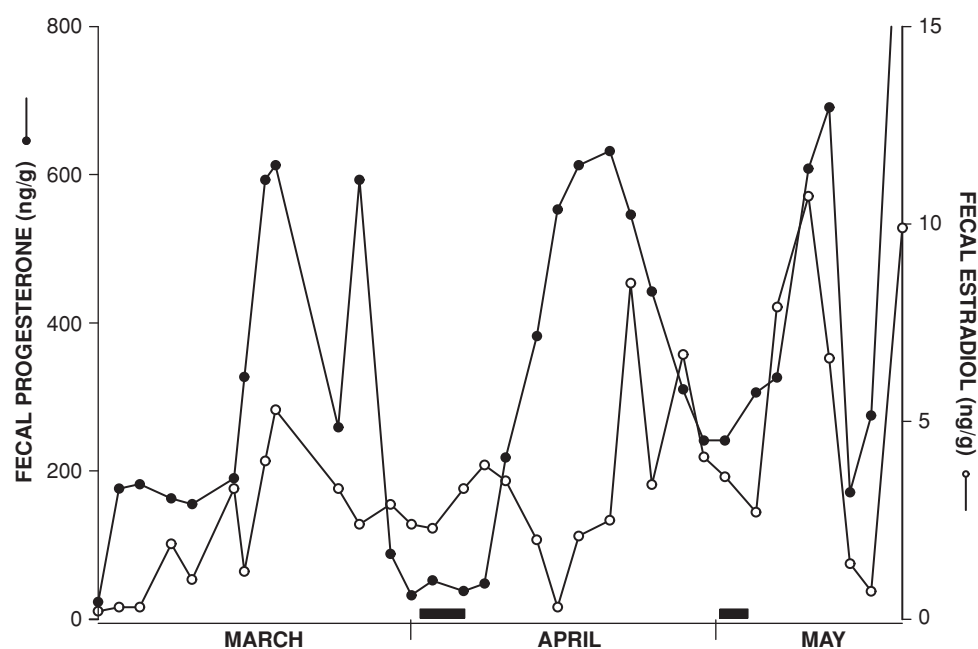


Figure 302.3 Patterns of fecal progesterone and estradiol concentrations during successive estrous cycles in a Grevy's zebra; bars indicate periods of mating.⁴

domestic horse.³² Mares that have failed to conceive by the end of the breeding season may cease to cycle and go into anestrus. The ovaries of anestrus mares are largely inactive, containing some small follicles and some tiny, regressed corpora lutea.

Mountain zebra

A detailed study of female reproduction in the Hartmann's zebra was conducted by Westlin-van Aarde *et al.*²² Ovaries and plasma were collected from free-ranging zebra mares shot in the Etosha National Park, Namibia. Both proestrous and estrus mares have an average of 16.8 smaller follicles (1–10 mm) and 1 larger follicle (either 21–30 or 31–40 mm) present in each ovary. Corpora lutea are not present. In diestrus, corpora lutea are formed and several small follicles (averaging 19 follicles per ovary) are still present. Follicular activity is similar in anestrus mares, with an average of 20 small follicles and 0 large follicles per ovary, but corpora lutea are not present. Intermediate-sized follicles (at 11–20 mm) are present at every stage.

Grevy's zebra

Captive Grevy's zebra mares at the Basle Zoo, Switzerland, were receptive for 2–9 days, in a 19–33-day cycle (ref. 33 in ref. 1). In the study by Asa *et al.*,⁴ females were receptive for 3 to 6 consecutive days, with an estrus cycle duration of 28 to 35 days. Simi-

larly, Smuts reported a 6-day estrus phase for mares in Kruger National Park, South Africa.

Asa *et al.*⁴ measured estradiol and progesterone in fecal samples from Grevy's zebra mares during consecutive estrus cycles to compare with courtship and mating behavior (Figure 302.3).

Gestation

Plains zebra

Gestation length in captive plains zebra at the Basle Zoo, Switzerland, was reported by Wackernagel³³ as 361–390 days, with an average of 371 days, in 28 pregnancies. At the Philadelphia Zoological Garden, USA,³⁴ reported gestation lengths of 341 and 355 days. These data are in accordance with those obtained from free-ranging animals by Klingel,⁶ at 378 and 385 days, and Smuts,² at 396 days. At 6–7 months prior to birth, a mare's abdomen is enlarged (when viewed posteriorly) and pregnancy is evident.^{2,35} Some pregnant horse mares have been reported to show estrus behavior,³⁶ which may also occur in zebras, so calculations of gestation length based on estrus behavior may not be reliable.

Mountain zebra

Gestation length in mountain zebra has been estimated at about 1 year. In the wild, a Cape mountain female was estimated to give birth after 359 days,⁷ and a Hartmann's female was estimated to give birth

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after 362 days.²¹ A captive Cape mountain zebra mare gave birth after 375 days.³⁷ These data are few, but given the gestation lengths of plains and Grevy's zebra, the figures are not unlikely.

Grevy's zebra

In the wild, gestation is longer in Grevy's zebra, averaging 390 days.^{1,38} Gestation lengths in captive animals have been shown to range from 358 to 438 days by Read *et al.*⁸ (St Louis, USA) and from 390 to 406 days by both Antonius³⁹ (Germany) and Kenneth⁴⁰ (England). Distension of the abdomen tends to be more apparent in Grevy's than in other zebra species.¹ Gestation length ranged from 391 to 406 days for mature captive mares but was 425 days for a young primiparous mare.⁴

Ovarian activity during gestation

Plains zebra

King¹ investigated ovarian activity during gestation in 20 free-ranging pregnant animals, postmortem. He found that until approximately 22 weeks of pregnancy, a corpus luteum of about 2.5 cm in diameter was present in one of the ovaries. After 22 weeks, it began to regress; at full term all that remained was a 0.3 cm wide strip extending approximately 0.9 cm from the ovarian fossa. Follicles of about 2 cm in diameter were present up to 17 weeks of pregnancy, decreased to 0.5 cm at 48 weeks, and showed renewed activity at full term, measuring 1 cm. Smuts² found similar results in the Kruger National Park zebras. During the first 190 days of pregnancy, he found a number of interesting phases of ovarian activity. After conception, ovarian activity gradually increased, reaching a peak between days 40 and 110. For the latter half of gestation, follicles larger than 12 mm were largely absent from the ovaries, although smaller, regressing follicles were often quite abundant. Active corpora lutea were a red-brown color, changing to yellow as they regressed.

According to Smuts,² activity was not equal in the two ovaries. The left ovary appeared to be more active than the right. In cases where mares produced all corpora lutea in only one ovary, a total of 109 were counted in the left and only 73 in the right (60% left and 40% right). In addition, the left ovaries of plains zebra mares were larger. Of 340 ovaries (170 pairs) measured, the left had a greater mass than the right in 120 instances (70.6% left > right). This was in contrast to King's results.¹ He found no difference in activity between the two ovaries, with active corpora lutea occurring in the right ovary in seven animals, and in the left ovary in eight animals.

Mountain zebra

During gestation, ovarian activity in the mountain zebra has been reported to be much like that of other zebra species. Joubert²¹ conducted a detailed study on free-ranging Hartmann's zebra females in which he found that large corpora lutea remained in the ovaries even at advanced stages of pregnancy (up to 5 months). The average size of the corpus luteum before reduction was 2.5 cm. The color changes of the corpus luteum were the same as in other zebra species, with active luteal bodies having a red-brown color before changing to yellow with advanced regression. Ovarian activity was reported to be equal in the two ovaries, with follicles maturing in either the left or the right, or more often in both ovaries.

Grevy's zebra

According to King,¹ gestational ovarian activity in free-ranging Grevy's mares is similar to that of plains zebra and mountain zebra.²¹ Until about 24 weeks of pregnancy, a corpus luteum of about 4 cm in diameter was present in one of the ovaries. By 34 weeks, the corpus luteum had regressed to about 1.7 cm, but persisted at 1.1 cm up to full term. This persistence of a fairly large corpus luteum during pregnancy was not associated with endocrine activity; total progesterone content of the corpus luteum decreased from 4750 µg at 8 weeks to 500 µg at 24 weeks. Follicular activity was considerable during early pregnancy (3 cm), but had ceased by 34 weeks. Follicles at 1 cm in diameter reappeared at 42 weeks and reached 3 cm by full term. As with plains and mountain zebra, active follicles were a dark red-brown color and changed to yellow as they regressed. For Grevy's females, ovarian activity appeared to be equal in the two ovaries, with corpora lutea forming in both the left (three animals) and right (three animals) ovaries.

Asa *et al.*⁴ measured levels of estradiol and progesterone excreted in feces throughout pregnancy (Figure 302.4) and found patterns similar to those reported for horses (e.g., Squires *et al.*⁴¹). They also measured equine chorionic gonadotropin (eCG) in urine, which also revealed a pattern similar to that seen in horses.⁴² Levels were in the detectable range beginning between 35 and 40 days gestation and returned to baseline between days 195 and 200. Ramsay *et al.*⁴³ also reported eCG elevations during that period of gestation.

Parturition

Plains zebra

Zebra mares give birth in much the same way as domestic horses. Wackernagel³³ reported information

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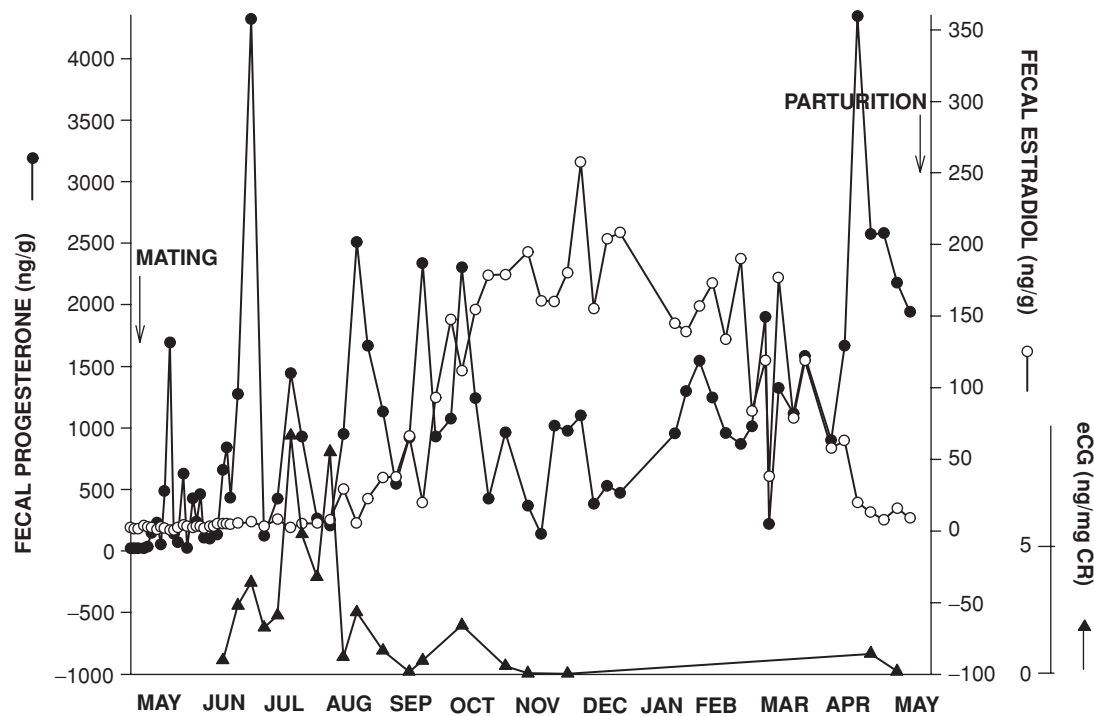


Figure 302.4 Patterns of fecal progesterone and estradiol and urinary equine chorionic gonadotropin concentrations during a conceptive estrous cycle followed by pregnancy in a Grevy's zebra.⁴ eCG, equine chorionic gonadotropin.

from captive animals, but a detailed account in the wild was recorded by Klingel.⁶ The mare was recumbent, lying flat on her side. The head and front legs of the foal had been expelled and were completely covered by the amnion. Parturition was completed 2 minutes later, at which time the mare sat up. The foal attempted to stand several times, breaking the amniotic sac and umbilical cord. After 14 minutes and four attempts, the foal stood successfully. The mare licked at and chewed the amniotic sac but did not eat any of it. The foal began to walk about, pulling out the placenta. In other instances observed, the placenta was not retained for more than 1.5 hours. After parturition, the mare and foal slowly rejoined their harem group, which ignored the birth and the presence of the newborn foal. In all instances recorded, the harem male remained within the vicinity of the foaling mare, between 10 and 50 m. Single births are the normal expectation although at least one instance of aborted twins has been recorded.³³ These accounts are consistent with the three stages of labor recognized in domestic equids,^{36,44} characterized by behavioral restlessness and the expulsion of the amniotic fluid in the initial stage, more predominant abdominal contractions and the expulsion of the foal in the second stage, and finally, expulsion of the placenta in the third stage.

Mountain zebra

Parturition has not been witnessed in mountain zebras,^{27,45} but is likely similar to that of other zebra species.

Grevy's zebra

As parturition approaches, a Grevy's female leaves the herd for the safety of heavier bush.⁴⁶ Birth normally takes place lying down, with the foal's hooves appearing first, and usually takes only about 7–8 minutes. The foal frees itself from the amnion and crawls towards the mother's head. The mother licks the foal clean, and unlike a plains zebra, ingests the membranes and some of the amniotic fluid,^{1,47} which may be important in initializing lactation or the mother-infant bond in this species.

Postpartum estrus

Plains zebra

Klingel²⁶ recorded the shortest intervals between two births as 378 and 385 days. The latency to foal heat has been reported to vary from 7 to 10 days after parturition.^{1,6,33} This combined with copulations by mares when their foals are only days old, indicates

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that plains zebra exhibit an estrus period only a few days after foaling.

Mountain zebra

Remnants of a corpus luteum, slightly larger than that seen at full term (averaging 2.55 cm), were found in the ovaries of a Hartmann's zebra female 3 to 6 weeks postpartum.²¹ This suggests an estrus 1 week after giving birth. Observations of animals at the Daan Viljoen Game Reserve, Namibia, showed the foaling-conception interval to vary between 3 and 7 weeks, indicating that conception does not generally take place during the first postpartum estrus in mountain zebra mares.

Grevy's zebra

According to King,¹ free-ranging Grevy's zebra mares showed a range of reproductive activity postpartum. Some animals exhibited evidence of estrus cycles from 2 to 16 weeks postpartum without conception, while others conceived between 3 weeks to 4 months postpartum. According to captive studies, at least one animal has been recorded as coming into estrus about 7 days after giving birth,⁸ and postpartum estrus has been estimated to last from 9 to 14 days.⁴⁸

Stallion

Behavior

In all three species of zebras the reproductive behavior of males involves interactions with females as well as breeding and bachelor males. To identify and locate females in estrus, males will often flehmen to scents deposited on the ground by the females. Once a male has found a female he will attempt to mount her; if successful he will consort with the female for varying degrees of time depending upon species. Interactions with bachelor males are typically aggressive, but depending on species, cooperation among breeding stallions is necessary to reduce cuckolding risk.¹⁰

Plains zebra

Plains zebras live in multi-tiered societies. One level consists of core social groups, such as closed membership harem groups and looser associations of bachelors, while another higher level, consists of herds comprising harem and bachelor groups that come together and break apart relatively frequently.^{10,12}

Herds form where resource abundance is high and where bachelor associations are numerous and strong. By banding together, stallions amortize the costs of driving away coordinated groups of cuckolded bachelors while providing their females with increased quality feeding time.

Mountain zebra

Like plains zebras, mountain zebras also have closed membership harems, and bachelor groups and herds will form. Although no details of the social dynamics of mountain zebra herds exist, it is likely that herd dynamics are similar to plains zebras.

Grevy's zebra

The open membership nature of Grevy's zebra groups reveals that relationships within and between the sexes are transitory. Males establish territories where all matings occur. Males, however, often leave their territories when no females are resident. Instead of searching for females, these males are searching for bachelors. By associating with them and reinforcing their dominance of territory, territorial males are able more easily to dominate and displace bachelors when they are present on territory with females.⁴⁸ Also, when on territory, stallions attempt to restrict estrus females from leaving their territories. While attempting to hold females hostage, males mount them frequently and ejaculate at hourly intervals, flushing previous sperm from a female's reproductive tract.⁹ This form of sperm competition is facilitated by the fact that Grevy's zebra males have disproportionately large testes for their body size.

Seasonality

Plains zebra

Adult plains zebra stallions in the Kruger National Park, South Africa, show a greater degree of reproductive activity during the summer months, particularly in January.³ This coincides with the mares' activity pattern where 85% of all foals are produced during the summer months, again with a peak in January.^{3,6} Testicle mass and seminiferous tubule diameter increase about 24% and 13%, respectively, from the months of lowest breeding activity to the peak months. Spermatogenesis is never completely absent, regardless of activity level. Despite these peaks in activity, it is clear that plains zebra are less seasonal than other African mammals, as foals are produced throughout the year.

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Mountain zebra

Mountain zebra stallions exhibit increased reproductive activity around the rains. At both the Mountain Zebra National Park (MZNP) and De Hoop National Reserve (DHNP), South Africa, Cape mountain zebra stallions show increased reproductive activity during the spring, with the majority of foals being produced the next spring/summer when the areas are flush with resources from either the summer (MZNP) or winter (DHNP) rains.²⁰ Similarly, Westlin-van Aarde *et al.*²² reported that in Etosha National Park, Namibia, the majority of reproductive activity in Hartmann's zebra stallions coincides with the start of the rains, occurring between November and April with a definite peak in February.²²

Grevy's zebra

For Grevy's zebra in northern Kenya, most reproductive activity occurs early in the long rains of June and July, with another, smaller peak of activity in the short rains of September and October. This behavior coincides with the onset of estrus in Grevy's mares, when they seek out and attract males.

Puberty and breeding life

Plains zebra

Puberty in the zebra stallion can be defined as 'the interval of time during which reproduction is possible, but terminating when full reproductive capability or sexual maturity is reached'⁵⁰ (but see Skinner⁵¹). At the Ngorongoro Crater, Tanzania, Klingel⁶ reported the youngest harem stallions to be between 5 and 6 years old, with most animals leaving their natal groups between the ages of 12 and 25 months, although some remained considerably longer (up to 4.5 years of age). In Kruger National Park, South Africa,³ the youngest harem stallion was 4 years old, and 80.8% of all harem stallions were between 4.5 and 12 years old. According to the Regional Studbook for North American Zoos, the youngest sire was only 8 months old when the mare conceived and another was only 10.5 months of age (Table 302.1).¹⁹

According to observations of captive animals, stallions are physiologically mature at 3 years of age.⁵² In the wild, the attainment of puberty seems to be a gradual process and sexual maturity comes later.³ Puberty was estimated to last from about 2.5 to 4.5 years of age. Spermatozoa were present in small numbers in animals aged 2.5–3 years, but appreciable numbers were not present until 3.5 years of age. Males were not socially mature (able to attract and acquire

females) until 4–4.5 years of age. Testicular mass increased most dramatically between the ages of 3 and 5 years old (from an average of 65 g to 302 g), while tubule development was more gradual, starting before the animals' first year (at an average of 40 μ m in diameter), and continuing into adulthood (to an average of 175 μ m in diameter). Upon reaching sexual maturity at about 4–4.5 years old, the combined testes mass reached 180 g and tubule development became relatively constant.

Smuts³ indicated that prime breeding stallions are under 12 years of age, but breeding does not stop in older animals, as indicated by King.¹ Stallions over 18 years old still lead harems. The oldest lead stallion recorded by Smuts² was 21 years old. The oldest male to sire young in North American zoos was almost 27 years old when the mare conceived (Table 302.1).

Mountain zebra

Puberty in Cape mountain zebra typically begins at about 4 to 4.5 years old, with most males attaining females at about 5 years of age.⁴⁵ A detailed study of testis mass and spermatogenesis of free-ranging animals was conducted by Penzhorn and Lloyd.²⁰ The testes of bachelor males aged 11, 24, and 29 months were prepubertal in histological appearance. Active spermatogenesis in the population began at about 4 to 4.5 years of age, but this was affected by daylength. Animals approaching 4 years of age during increasing daylength conditions showed more activity than did animals approaching 4 years of age during decreasing daylength conditions. The social environment was also important. In the absence of adult males, a Cape mountain zebra colt running with mares sired a foal when only 3.5 years old.

The testis mass of adult Cape mountain zebra in Mountain Zebra National Park was found to be appreciably less (at ~70 g) than that of other zebra species.²⁸ The mean mass of both testes plus their epididymides was 166.4 g. In eight of nine specimens, the right testis was consistently heavier than the left. This is in contrast to what has been seen in plains zebra males.³ The mean diameter of the seminiferous tubules was shown to increase rapidly between 2 and 6 years of age before leveling off.

In Hartmann's zebra, the average weight of the testis at 87.6 g is also markedly smaller than that of the plains or Grevy's zebra. According to Joubert,²¹ testis size varied with season, reaching a maximum size (99.4 g) in January and a minimum size (83.1 g) in September. The testes started increasing in weight at about 2 years of age, reaching their maximum size at around 3.5 years of age.

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Grevy's zebra

Free-ranging Grevy's zebra males reach puberty at about 4 years of age.¹ At this stage, males are likely to be living in bachelor groups, not consorting with mares and foals until a year or two later. Captive animals in England and in Kenya reached puberty between 3 and 4.5 years, but exhibited low conception rates until about 6 years of age. Read *et al.*,⁸ however, found that in the USA captive males could achieve sexual potency at ages as young as 7 months, and that one captive animal bred until 18 years of age. More recent data from the International Studbook document that the youngest males able to sire young were 2 years of age at the time the mares conceived, and that the oldest was almost 26 years (Table 302.1).²⁵

King¹ studied the testis size and weight of free-ranging Grevy's zebra in some detail. The testis of a young adult Grevy's zebra, measuring about 11.5 × 8.5 × 7.5 cm and weighing about 475 g, is significantly larger than that of the plains or mountain zebra. According to King, testis size and weight in the Grevy's male varied with reproductive state. A territorial male's testis weight was recorded at 600 g, while the testis weight of an older male associated with a mixed herd was recorded at 550 g.¹ The testosterone content of these animals also varied, with the young male, the territorial male, and the aged male having 154, 41.5, and 59 mg/100 µg of testis, respectively.

The male reproductive organs

Plains zebra

The male reproductive organs of culled animals were studied in detail by King.¹ The testes are carried in the scrotum, which hangs between the thighs and posterior to the penis. The deferent duct passes up from each testis, through the inguinal canal to the accessory organs that lie on the ventral floor of the pelvic cavity. The ducts (0.4 cm in diameter) enlarge to form the ampullae (1.2 cm in diameter) as they pass back over the dorsal surface of the bladder and open at the beginning of the urethra. The sac of the seminal vesicle opens into the urethra behind each ampulla anterior to the prostate gland. The prostate gland is a lobulated, bilobed gland extending 2.5 cm on each side of the urethra. The bulbourethral glands are located about 3 cm posterior and lateral to the urethra at the base of the penis. The urethra passes around the posterior border of the pubic symphysis into the penis and extends along the ventral surface of the abdomen. The extremity of the urethra is enclosed within the prepuce and lies in the region of the umbilicus.

Mountain zebra

The most marked feature of the male reproductive organs in mountain zebra is the size of the testis. At an average of 70 g and 86 g for Cape mountain and Hartmann's zebra, respectively, the mountain zebra testis is appreciably smaller than that of either the plains or Grevy's zebra.^{21,28}

Grevy's zebra

Even when controlling for animal size, the male accessory organs are much larger in Grevy's zebra than in the plains or mountain zebra.^{1,21,28} The most conspicuous feature is the large seminal vesicle, which can contain up to 400 mL of fluid in the largest stallion sampled, and up to 1 liter in a captive animal at about 15 years of age. Testis size and weight are also significantly greater and vary with reproductive state of the male (see above).

Foal

Plains zebra

Single births were recorded by Klingel and Klingel⁵³ in the wild and by Wackernagle³³ in captivity. Klingel calculated sex ratios for the foals born in the Ngorongoro Crater, Tanzania. Of the 170 foals born, 87 were females and 74 were males, giving a ratio not different from 1:1. Foals extricated themselves from the birth membranes unaided, stood within 11 to 13 minutes, stepped after 19 minutes, walked after 32 minutes, and cantered after 44 to 60 minutes. In the one instance of actual foaling recorded by Klingel,²⁶ the offspring suckled for the first time within 1 hour, and 12 more times in the next 4 hours for 30 s to 2.5 min a time for a total of 14 min. Wackernagle³³ reported first suckling at 71 min after parturition.

During the first few days to weeks of the foal's life, the mother is very protective. This correlates with the imprinting period in which the foal learns to recognize its mother by her call, her scent, and her stripe pattern. Until imprinting is complete, the foal will follow any large object, including vehicles,⁶ and the mare's protectiveness insures that the foal will not imprint on another animal. During this period, other members of the group (including the harem stallion) are not allowed to approach the foal too closely. In fact, other females have been seen attempting to kill newborns.⁵⁴ Beyond this period, the mother and foal remain close, but others are allowed to interact and socialize with the foal. Mothers with young foals are more wary than other members of the group and are the first to move off at signs of danger.

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Mountain zebra

Actual births of mountain zebra foals have not been recorded in the wild,^{21,27,55} but data regarding sex ratio at birth, mare-foal behavior, and foal activity do exist. The sex ratio at birth is not different from 1:1 in either Cape mountain or Hartmann's zebra, and the young are just as precocious, getting up, walking, and running within a short period of time.⁷

During the first few weeks of life, mountain zebra foals and their mothers behave very much like other zebra species. Both Cape mountain and Hartmann's zebra foals remain close to their mothers in the first weeks. In the first few hours after birth, Hartmann's zebra mares spend much time sniffing and licking the foal. This may be important to insure the female's recognition of its young.⁵⁶ Both Cape mountain and Hartmann's zebra foals make frequent tactile contact with their mothers, rubbing their faces along their mothers' flanks, initiating naso-nasal contact, and nibbling at their necks. In both subspecies the mothers actively prevent contact between the foal and other members of the group. This can be taken to extremes in Hartmann's zebra as some mothers will remain separate from their groups for several days.²⁷ As in plains and Grevy's zebra, this behavior is correlated with the critical period of imprinting of the mare's sound, scent, and stripe pattern onto the foal. Mares of both species are more skittish than other group members and are the first to flee at any sign of danger.

Grevy's zebra

Grevy's zebra foals are similar to both plains and mountain zebra foals. Single births have been recorded both in the wild¹ and in captivity.⁸ Data from captive animals show that the young are precocious, standing 6–14 min after birth, walking by 30 min, and running by 45 min. At about 29 min the foal attempts to nurse, and does so by 69 min. At 97 min the foal stands well and at 2 hours nurses well. In captivity, the sex ratio at birth is 1.09:1.⁵

The Grevy's newborn will follow any large, moving object. The mother is quite protective (particularly during the first 2 days) and keeps other animals away until her offspring has imprinted upon her call, scent, and stripe pattern. After imprinting has been achieved, the mother and foal will join a group of nursing mothers. When traveling to water, the mare will sometimes leave the foal with this group.³⁸

Weanling

Plains zebra

According to Smuts,² lactation generally continues until 1 to 2 months before the birth of the next foal.

The earliest weaning occurred at 11 months of age, but if a mare does not conceive soon after foaling, she will continue to suckle her foal throughout and beyond its first year. One captive mare suckled her foal until it was 16 months old, weaning it 6 months prior to the birth of her next foal.

Mountain zebra

On average, mountain zebra foals are weaned at about 10 months of age,²⁷ about 3.5 to 6 months before the new foal is born. For Cape mountain zebra, the timing of weaning is highly dependent on the birth of new offspring and can be quite variable, but for Hartmann's zebra, 10 months seems to be the norm. If mares do not conceive during postpartum estrus, suckling may be permitted for longer periods. Penzhorn^{45,57} reported infrequent suckling in animals as old as 20 months of age.

Grevy's zebra

Grevy's zebra foals are weaned at about 9 months (32–42 weeks¹), but will remain with their mothers for several more months or years, depending on the sex (see below). The young are semi-independent at about 7 months, often being left by the mother or leaving her for hours at a time.

Yearling

Plains zebra

Young mares at the age of 1–2 years, around the time of their first heat, are abducted from their families by stallions. Klingel⁶ reported that on average, mares were abducted at about 18 months, but as young as 13 months of age. These young females do not typically remain with the initial stallion, but within about 6 months of separating from their natal group, become permanent members of a reproductive group.

Most young stallions leave the natal group at about 12–25 months of age, in some cases later, and either stay single or join other stallions to form bachelor groups. Bachelor groups are of variable numbers, up to 15 animals. Smaller groups of two, three, and four have been reported to be very stable. Departure of the young males is not correlated with sexual maturity or any antagonism with the lead stallion, but seems to be determined more by the composition of the natal group. In particular, the males tend to leave after the birth of their mothers' next foal.

Mountain zebra

The timing of dispersal is similar for males and females for both Cape mountain and Hartmann's

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zebras. In Mountain Zebra National Park, male and female Cape mountain zebras left their natal groups at an average of 21.85 months.^{45,57} In De Hoop Nature Reserve, however, females leave their groups earlier, at 18.85 months, than do the males, at 24.36 months.¹⁷ Female dispersal coincides with estrus onset, but there is no physiological correlate in males. In both MZNP and DHNR, the foals leave the group of their own accord and are not forced to do so by either the stallion or the mare. In addition, dispersal is not correlated with the mothers' subsequent pregnancies or her status,¹⁷ and stallions in MZNP will vigorously attempt to retain the foals.^{45,57} Dispersal in young mountain zebra is likely due to bond transference from maternal/paternal to age cohort associations. This is similar to what Klingel⁶ reported in plains zebra.

In stark contrast, Hartmann's zebra foals typically leave the natal group at around 14 to 16 months of age.²⁷ At this stage (shortly before the birth of her next foal), the mare actively tries to drive the older foal (whether male or female) out of the group. Approximately one-third of the foals leave the group as a direct result of this aggressive behavior. The remaining two-thirds leave of their own accord, sometimes as much as 2 years later. Upon the birth of her next foal, the mare will ignore the older foal if it has not already left.

Young Cape mountain mares often join bachelor groups before joining a more stable, reproductive group. This was always the case for mares in De Hoop Nature Reserve mares,¹⁷ and very often the case for mares in Mountain Zebra National Park.^{45,57} At DHNR, the females stay in the bachelor groups approximately 8.7 months, leaving when they are about 29.9 months old. The females are not abducted by harem stallions; they leave of their own accord. At MZNP, females will sometimes remain solitary for several months before joining either bachelor or reproductive groups. Older mares are taken up by harem stallions sooner, while younger mares are either solitary or in bachelor groups for longer periods.

Young Cape mountain males in DHNR stay in their natal groups longer than the females, for an average of 24.36 months, leaving when they are about 52.44 months of age.¹⁷ These data agree with Penzhorn's^{45,57} estimate of the age at sexual maturity. In the MZNP, young males roam singly or in unstable bachelor groups only loosely associated with the more stable bachelor groups.⁵⁷ Affiliation with the natal group is strong; young males having left after the displacement of their fathers will often join them. In addition, young males having left their natal group still intact, will often rejoin the group for short periods.

Hartmann's zebra females are typically herded by either bachelors, forming the core unit of a new reproductive group, or by harem stallions, thereby in-

tegrating into an already stable reproductive group. Young males leave their natal group to join bachelor groups that consist of mostly young, but also older, displaced stallions.²⁷

Grevy's zebra

Young mares leave their mothers at about 13–18 months of age, typically 2–7 months into the mothers' next pregnancy.¹ The females will not breed until they are between 2 and 4 years old. During their first estrus (at around 4 years of age), the males they attract separate them from their mothers to mate.⁵⁸ More experienced mares will present only to territorial males, causing less disruption to the female groups.

Grevy's males stay with their mothers until they are about 3 years old, after which they join a bachelor group or a mixed herd.¹ Young males do not typically gain access to females until they are about 5 years old, so have a bachelor period of 2 to 5 years.⁶

References

1. King JM. A field guide to the reproduction of the Grant's zebra and Grevy's zebra. *East African Wildlife Journal* 1965;3: 99–117.
2. Smuts GL. Reproduction in the zebra mare (*Equus burchelli antiquorum*) from the Kruger National Park. *Koedoe* 1976;19:89–132.
3. Smuts GL. Reproduction in the zebra stallion (*Equus burchelli antiquorum*) from the Kruger National Park. *Zoologica Africana* 1976;11:207–20.
4. Asa CS, Bauman JE, Houston EW, Fischer MT, Read B, Brownfield CM, Roser JF. Patterns of excretion of fecal estradiol and progesterone and urinary chorionic gonadotropin in Grevy's zebras (*Equus grevyi*): ovulatory cycles and pregnancy. *Zoo Biology* 2001;20:185–95.
5. Dobroruka LJ, Holejskova A, Maslova I, Novotny V. An analysis of the population of Grevy's zebra (*Equus grevyi*) in Dvur Kralove Zoo. *International Zoo Yearbook* 1987;26:290–3.
6. Klingel H. Reproduction in the plains zebra, *Equus burchelli boehmi*: behavior and ecological factors. *J Reprod Fertil Suppl* 1969;6:339–45.
7. Penzhorn BL. Reproductive characteristics of a free-ranging population of Cape mountain zebra (*Equus zebra zebra*). *J Reprod Fertil* 1985;73:51–7.
8. Read B, Kelly C, Bueler M, Junge R. Grevy's zebra management survey. In: American Association of Zoological Parks and Aquariums, Species Survival Plan. St Louis, MO: St Louis Zoological Park, 1988; pp. 160.
9. Ginsberg JR, Rubenstein DI. Sperm competition and variation in zebra mating behavior. *Behav Ecol Sociobiol* 1990; 26:427–34.
10. Rubenstein DI, Hack M. Natural and sexual selection and the evolution of multi-level societies: insights from zebras with comparisons to primates. In: Kappeler P, Schaik CP v (eds) *Sexual Selection in Primates: New and Comparative Perspectives*. Cambridge University Press, 2004; pp. 266–79.

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11. Klingel H. A comparison of the social organization of equids. In: Proceedings of a Conference on the Ecology and Behavior of Feral Equids. University of Wyoming, Laramie, 1979.
12. Rubenstein DI. Ecology and sociality in horses and zebras. In: Rubenstein DI, Wrangham RW (eds) *Ecological Aspects of Social Evolution: Field Studies of Birds and Mammals*. Princeton, NJ: Princeton University Press, 1986; pp. 282–302.
13. Rubenstein DI. The ecology of female social behavior in horses, zebras and asses. In: Jarman P, Rossiter A (eds) *Animal Societies: Individuals, Interactions and Organisations*. Kyoto: Kyoto University Press, 1994; pp. 13–28.
14. Rubenstein DI, Nuñez C. Sociality and reproductive skew in horses and zebras. In: Hager R, Jones CB (eds) *Reproductive Skew in Vertebrates: Proximate and Ultimate Causes*. Cambridge University Press, 2009; pp. 196–226.
15. Ginsberg JR. The ecology of female behaviour and male mating success in the Grevy's zebra. *Symp Zool Soc Lond* 1989;61:89–110.
16. Rowen M. Mother–infant behavior and ecology of Grevy's zebra, *Equus grevyi*. New Haven, CT: Yale University, PhD thesis, 1992.
17. Lloyd PH, Rasa OAE. Status, reproductive success and fitness in Cape mountain zebra (*Equus zebra zebra*). *Behav Ecol Sociobiol* 1989; 25:411–20.
18. Fischhoff IR, Sundaresan SR, Cordingley J, Larkin HM, Sellier M-J, Rubenstein DI. Social relationships and reproductive state influence leadership roles in movements of plains zebra (*Equus burchellii*). *Anim Behav* 2007;73:825–31.
19. Minot J. *Plains Zebra North American Regional Studbook*. Atlanta, GA: Zoo Atlanta, 2004.
20. Penzhorn BL, Lloyd PH. Comparisons of reproductive parameters of two Cape mountain zebra (*Equus zebra zebra*) populations. *J Reprod Fertil* 1987;35:661–3.
21. Joubert E. Notes on the reproduction in the Hartmann zebra *Equus zebra hartmannae* in South West Africa. *Madoqua* 1974;8:31–5.
22. Westlin-van Aarde LM, van Aarde RJ, Skinner JD. Reproduction in female Hartmann's zebra, *Equus zebra hartmannae*. *J Reprod Fertil* 1988;84:505–11.
23. Kingdon J. *East African Mammals; an Atlas of Evolution in Africa*. Chicago, IL: University of Chicago Press, 1979.
24. Williams SD. Grevy's zebra: Ecology in a heterogeneous environment. PhD thesis, University College London, 1998.
25. Langenhorst T. *Grevy's Zebra International Studbook*. Winchester, UK: Marwell Zoo, 2004.
26. Klingel H. Notes on the biology of the plains zebra *Equus quagga bohemii matschie*. *East African Wildlife Journal* 1965;3:86–8.
27. Joubert E. The social organization and associated behaviour in the Hartmann zebra *Equus zebra hartmannae*. *Madoqua* 1972;6:17–56.
28. Penzhorn BL, van der Merwe NJ. Testis size and onset of spermatogenesis in Cape mountain zebras (*Equus zebra zebra*). *J Reprod Fertil* 1988;83:371–5.
29. Benesch F, Wright J. *Veterinary Obstetrics*. London: Baillière, Tindall, and Cox, 1957.
30. Asa CS. Equid reproductive biology. In: Moehlman PD (ed.) *IUCN/SSC Equid Action Plan*. Gland, Switzerland: IUCN, 2002; pp. 113–17.
31. Kupfer M. The sexual cycle of female domesticated mammals. In: Department of Agriculture 13th and 14th Reports of the Director of Veterinary Education and Research, 1928, pp. 1211–70.
32. Hammond J, Wodzicki K. Anatomical and histological changes during the oestrous cycle in the mare. *P Roy Soc Lond B Bio* 1941;130:1–23.
33. Wackernagel H. Grant's zebra *Equus burchelli boehmi*, at Basle Zoo – a contribution to breeding biology. *International Zoo Yearbook* 1965;5:38–41.
34. Brown CE. Rearing wild animals in captivity and gestation periods. *J Mammal* 1936; 17:10–13.
35. Smuts GL. Pre- and postnatal growth phenomena of burchell's zebra (*Equus burchelli antiquorum*). *Koedoe* 1975; 18:69–102.
36. Asa CS, Goldfoot DA, Ginther OJ. Assessment of the sexual behavior of pregnant mares. *Hormon Behav* 1983;17:405–13.
37. Penzhorn BL. Behaviour and population ecology of the Cape mountain zebra *Equus zebra zebra* Linn, 1758 in the Mountain Zebra National Park. Pretoria: University of Pretoria, DSc thesis, 1975.
38. Groves CP. *Horses, Asses, and Zebras in the Wild*. Newton Abbott and London: David and Charles, 1974.
39. Antonius. Einige bemerkenswerte Zuchterfolge in Schonbrunn im Jahre 1931. *Zoological Garten* 1932;5:91–7.
40. Kenneth JH. *Gestation Periods*. Slough, UK: Commonwealth Agricultural Bureau, 1953.
41. Squires EL, Douglas RH, Steffenhagen WP, Ginther OJ. Ovarian changes during the estrous cycle and pregnancy in mares. *J Anim Sci* 1974;38:330–8.
42. Roser JF, Lofstedt RM. Urinary eCG patterns in the mare during pregnancy. *Theriogenology* 1989;32:607–22.
43. Ramsay EC, Moran F, Roser JF, Lasley BL. Urinary steroid evaluations to monitor ovarian function in exotic ungulates: X. Pregnancy diagnosis in *Perissodactyla*. *Zoo Biology* 1994;13:129–47.
44. Ginther OJ. *Reproductive Biology of the Mare: Basic and Applied Aspects*, 2nd edn. Cross Plains, WI: Equiservices, 1992.
45. Penzhorn BL. A long-term study of social organisation and behaviour of Cape mountain zebras *Equus zebra zebra*. *Zeitschrift für Tierpsychologie* 1984;64:97–146.
46. Churcher CS. *Equus grevyi*. *Mammalian Species* 1993; 453:1–9.
47. King JM, Short RV, Mutton DE, Hamerton JL. The reproductive physiology of male zebra-horse and zebra-donkey hybrids. *Symp Zool Soc Lond* 1966;15:511–27.
48. Nelson L. Equidae. In: Fowler ME (ed.) *Zoo and Wild Animal Medicine*. Philadelphia, PA: W.B. Saunders and Co., 1986; pp. 926–31.
49. Ginsberg JR. Social organization and mating strategies of an arid adapted equid: The Grevy's zebra. Princeton, NJ: Princeton University, PhD thesis, 1988.
50. Emmens CW. Physiology of gonadal hormones and related synthetic compounds. In: Cupps CaPT (ed.) *Reproduction in Domestic Animals*. London: Academic Press, 1969.
51. Skinner JD. The concept of puberty. *S Afr Med J* 1969;43: 1–420.
52. Trumler E. Beobachtungen an den Bohmzebras des George von Opel Freigeheges für Tierforschung. *Saugetierk Mitt* 1958;6:1–48.
53. Klingel H, Klingel U. Die Geburt eines Zebras (*Equus quagga bohemii Matschie*). *Zeitschrift für Tierpsychologie* 1966;23:72–6.
54. Fischhoff IR, Sundaresan SR, Larkin HM, Cordingley JE, Sellier M-J, Rubenstein DI. A rare fight between two female plains zebra (*Equus burchelli*). *J Ethol* 2010;28:201–5.

Zebra Reproduction 2865

55. Joubert E. Size and growth as shown by pre- and post-natal development of the Hartmann zebra *Equus zebra hartmannae*. *Madoqua* 1974;8:55-58.
56. Ewer RF. *Ethology of Mammals*. New York: Plenum Press, 1968.
57. Penzhorn BL. Observations of mortality of free-ranging Cape mountain zebra *Equus zebra zebra*. *S Afr J Wildl Res* 1984;14:89-90.
58. Churcher CS. Grevy's: the other zebra. *Swara* 1982;5:12-18.

