

Odocoileus hemionus. By Allen E. Anderson and Olof C. Wallmo

Published 27 April 1984 by The American Society of Mammalogists

***Odocoileus hemionus* (Rafinesque, 1817)**

Mule Deer

- Cervus hemionus* Rafinesque, 1817:436. Type locality near mouth of the Big Sioux River, South Dakota.
- Cervus auritus* Warden, 1820:640. Type locality "... la contré situé a l'ouest des montagnes Rocky, piès des bords de la rivière de Koooskooské."
- Cervus macrotis* Say, 1823:88. Type locality Mora River, near present town of Mora, New Mexico.
- Cervus Lewisii* Peale, 1848:39. Applied to specimens from Feather River and San Francisco Bay, California.
- Cariacus punctulatus* Gray, 1852:239. Type locality California.
- Cervus richardsoni* Audubon and Bachman, 1848:table of contents and plate 106. Type locality California.
- Eucervus pusilla* Gray, 1873:157. Type locality North America (perhaps British Columbia).
- Dorcelaphus crooki* Mearns, 1897:2. Type locality summit Dog Mts., 6,129 feet, Hidalgo County, New Mexico.
- Cariacus virgultus* Hallock, 1899:404. Type locality near Hallock, Kittson County, Minnesota.

CONTEXT AND CONTENT. Order Artiodactyla, Family Cervidae, Subfamily Odocoileinae, Tribe Odocoileini. The genus *Odocoileus* includes two extant species, *O. hemionus*, as defined here, and *O. virginianus* (= *Dama virginiana* Zimmerman, 1780) that occurs over most of the southern half of North America and southward to northern South America and is sympatric with *O. hemionus* in much of the western half of North America. Subspecies recognized by Hall (1981) and Wallmo (1981a) are:

- O. h. californicus* (Caton, 1876:464). Type locality near Gaviota Pass, 40 mi W Santa Barbara, Santa Barbara County, California. California mule deer.
- O. h. cerrosensis* Merriam, 1898:101. Type locality Cedros Island, west coast of Baja California, Mexico. (Wallmo, 1981a, suggested that the distinction of *cerrosensis* from *peninsulae* be reconsidered). Cedros Island deer.
- O. h. columbianus* (Richardson, 1829:257). Type locality Cape Disappointment, Pacific County, Washington (*lewisii* Peale, *punctulatus* Gray, *richardsoni* Audubon and Bachman, *pusilla* Gray, and *scaphiotus* Merriam are synonyms). Columbian black-tailed deer.
- O. h. crooki* (Mearns, 1897:468). Type locality Dog Mountains, Hidalgo County, New Mexico (*eremicus* Mearns and *canus* Merriam are synonyms according to Hoffmeister, 1962, although Hall, 1981, recognized *O. h. eremicus*).
- O. h. fuliginatus* Cowan, 1933a:326. Type locality Barona Ranch, 30 mi E San Diego, San Diego County, California. Southern mule deer.
- O. h. hemionus* (Rafinesque, 1817:436). Type locality near mouth of Big Sioux River, South Dakota (*auritus* Warden, *macrotis* Say, *montanus* Caton, and *virgultus* Hallock are synonyms). Rocky Mountain mule deer.
- O. h. inyoensis* Cowan, 1933b:69. Type locality 10 mi W Big Pine, Inyo County, California (pers. comm. from I. McT. Cowan, W. Macgregor, and A. S. Leopold, to O. C. Wallmo question the validity of *inyoensis*). Inyo mule deer.
- O. h. peninsulae* (Lydekker, 1898:900). Type locality between La Laguna and Victoria Mountain, Sierra Laguna, Baja California, Mexico. Peninsula mule deer.
- O. h. sheldoni* Goldman, 1939:497. Type locality Tiburon Island in Gulf of California, Sonora, Mexico. (Wallmo, 1981a, suggested that the distinction of *sheldoni* from *peninsulae* be reconsidered). Tiburon Island mule deer.
- O. h. sitchensis* Merriam, 1898:100. Type locality Sitka, Alaska. Sitka black-tailed deer.

DIAGNOSIS. The following characters define the genus (Cowan, 1936; Hall, 1981): face long and narrow; rhinarium well developed; vomer high, dividing nostrils into two chambers posteriorly; upper canines usually absent; lacrimal pits and preorbital glands small; two lacrimal ducts on rim of orbit (Fig. 1); antlers normally present only in males, beam rising at marked angle to plane of face; generally dichotomously forked, with subbasal snag; anterior prong of main forks usually larger than posterior prong; main prongs with secondary forking. Skull, teeth, and antler characters do not reliably discriminate between all forms of *O. hemionus* and *O. virginianus* (Cowan, 1956a). Ears variable in size and hairiness; tarsal and metatarsal glands present; interdigital glands present on both fore- and hindfeet; novicolocuboid of tarsus free from cuneiform; coat uniformly colored; young spotted.

Odocoileus hemionus is distinguished from *O. virginianus* by a tail that is white to black above and tipped with black (in opposition to tail brown above, fringed with white laterally, and white below), ears approximately $\frac{2}{3}$ length of head (as opposed to $\frac{1}{2}$ length of head), antlers that branch dichotomously (Fig. 2) rather than one main beam with vertically rising tines, no external indication of the interdigital glands in contrast to orifices surrounded by white hairs, and deeper (ca 23 mm) preorbital pits. Metatarsal glands more than 25 mm in length separate *O. hemionus* from *O. virginianus* (Hall, 1981). The northern forms of *Odocoileus* spp. may have larger metatarsal glands (Anderson et al., 1964; Cowan, 1956a; Hershkovitz, 1958).

The western subspecies, or black-tailed deer (*O. h. columbianus* and *O. h. sitchensis*), have amply haired tails and raise them in flight, as does *O. virginianus*, but they do not wave them from side to side as the latter does. Geist (1981) described the unique bounding gait of *O. hemionus* as stotting. Stotting is a highly modified gallop (Eslinger, 1976), common in mule deer and, to a lesser extent, in Columbian black-tailed deer. In Sitka blacktails, stotting apparently is seen rarely. Stotting may be an alarm behavior that alerts conspecifics. Mule deer and white-tailed deer have essentially the same gallop but mule deer may lack the speed of whitetails (Geist, 1981).

GENERAL CHARACTERS. *Odocoileus hemionus* is a medium-sized cervid; adult males stand about 1 m at the shoulders and commonly attain 70-150 kg live weight (Fig. 2). The pelage of the back and sides ranges from gray to dark brown, or even black in median dorsal zone. The summer coat is more reddish-brown. According to Geist (1981), individual mule deer range from dark brown gray, dark and light ash-gray to brown and even reddish; the rump patch may be white or yellow and some have one white throat patch, but others have two. The white tails of most mule deer terminate in a tuft of black hair, or less commonly in a thin tuft of white hairs, or the barest admixture of black hairs. On other mule deer a dark dorsal line runs from the back down the top of the tail to the black tail tip. All markings vary considerably among individuals, but remain constant throughout life. A V-shaped dark mark extends from a point between the eyes upward and laterally; it is more characteristic and more conspicuous in males.

Growth in *O. h. hemionus* in Colorado (Anderson et al., 1974) was roughly parallel in males and females the first year. Thereafter, males, in general, exceeded females in carcass weight, chest girth, neck circumference, body length, head length, cranial breadth, shoulder height, hindfoot length, and hoof length. The largest male (bled carcass weight) was 112.3 kg and the largest female 75.2 kg; in shoulder height, the largest male was 106 cm and the largest female 100 cm (Anderson et al., 1974).

DISTRIBUTION. *Odocoileus hemionus* occurs over most of North America west of the 100 meridian from 23° to 60°N (Fig. 3). The most southerly records are from northern San Luis Potosi, Mexico (Cowan, 1956a) and the most northerly from southern

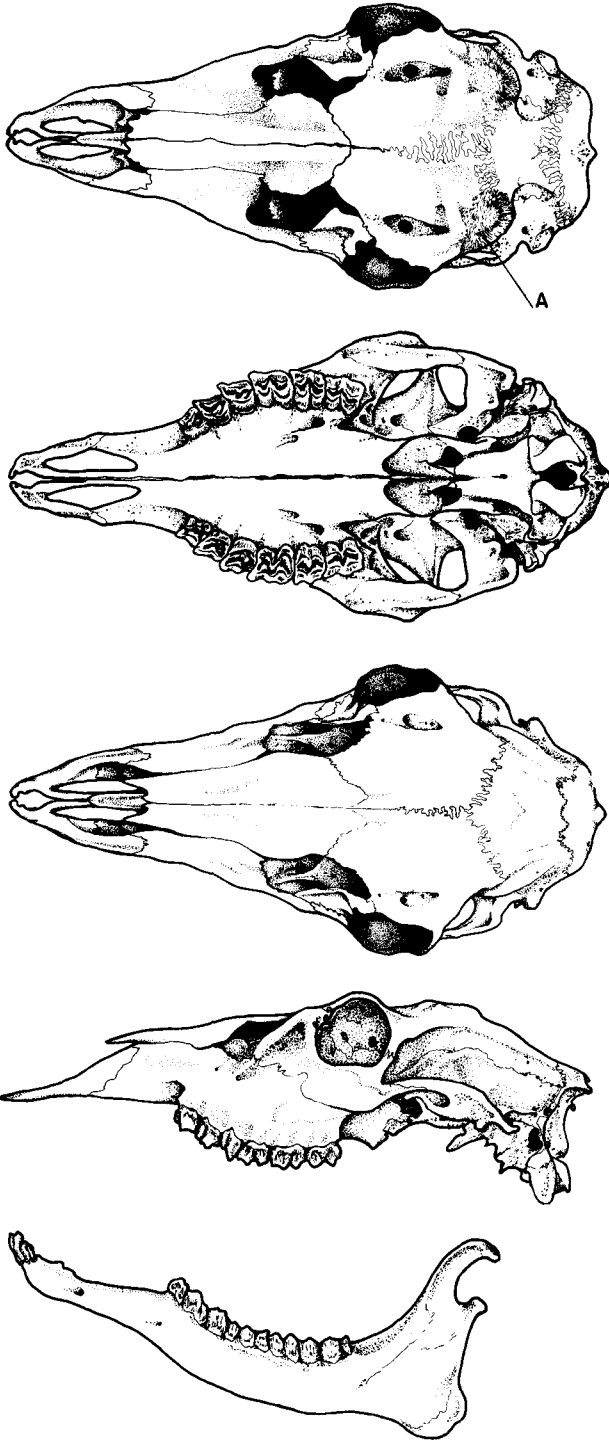


FIGURE 1. Dorsal and ventral views of cranium of male *Odocoileus hemionus hemionus* with antler pedicel (A) denoted (Dept. Anatomy, Colorado State Univ.), and dorsal and lateral views of cranium and lateral view of mandible of female (UCM 5387, from Converse County, Wyoming). Drawn by Gwen A. Anderson.

Yukon Territory, Canada (Wallmo, 1981a) but boundaries are provisional. The eastern edge of the usually occupied range extends from southwestern Saskatchewan through central North and South Dakota, Nebraska, Kansas, and western Texas, but isolated occurrences are reported from Minnesota, Iowa, and Missouri (Wallmo, 1981a). Major gaps in geographic distribution are in the Mojave and Sonoran deserts in southern Nevada, southeastern California, southwestern Arizona and northwestern Sonora, the Central Valley of California, and probably the Great Salt Lake desert region. Oth-



FIGURE 2. Three male Rocky Mountain mule deer (*Odocoileus hemionus hemionus*). Photo by Geoffrey Tischbein, Colorado Division of Wildlife.

erwise, the species occurs in all of the biomes of western North America north of central Mexico, except the Arctic tundra.

FOSSIL RECORD. The earliest fossil remains of *Odocoileus* in North America, from Arizona, California, and Kansas, were estimated to be ≥ 2 million years old (mid- to late Pliocene), and the genus was speculated to be of Old World origin (Opdyke et al., 1977). An early Blancan (late Pliocene) antler base from southwestern Washington, assigned to *Odocoileus ensifer* (Cope), was recognized by Fry and Gustafson (1974) as similar to a recent specimen of *O. hemionus*, though they considered *O. ensifer* to be distinct. A basal portion of an antler from late Pliocene deposits in the San Francisco Bay region compared well with recent specimens of *O. hemionus* (Savage, 1951). Pleistocene fragments of antler, teeth, and lower jaw (from near Aguascalientes in central Mexico) that resembled *O. hemionus* were referred to *O. ensifer* (Mooser and Dalquest, 1975). The fossil trace of *O. hemionus* is poor until it appears abundantly in recent sites within its present range. The race with the largest distribution, *O. h. hemionus*, now occupies an area that was covered by ice in the Pleistocene, whereas several races occur to the south where glaciation was either limited or did not occur (Cowan 1956a).

FORM AND FUNCTION. Cowan and Raddi (1972) identified four types of adult hairs and the annual cycle of follicles producing the natal, juvenile, adult summer and adult winter pelages. The pelage of adult deer is composed of woolly underhairs, mane type hairs (18 to 44 mm in length), intermediate guard hairs of the same length and the major component of the pelage, and large guard hairs up to 80 mm in length. Guard hairs have a sensory function and are distributed over the body about 2 cm apart and appear first for each molt. Among fawns, the characteristic white spots disappeared at 83 to 87 days and the pelage turned gray at 92 to 98 days (Robinette et al., 1977). Among adults, two hair cycles are completed annually, alternating between a summer pelage for 5 months and a winter pelage for 7 months. The abundance of woolly underhair in winter and its absence in summer is largely

responsible for the distinctly different coloration of winter and summer pelages (Cowan and Raddi, 1972).

The udder has four separate quarters each with a single teat and teat canal. The posterior quarters are the largest (Mueller and Sadleir, 1977). The udder averaged 12 cm long, 11 cm wide, and 4 cm deep, with teat lengths of 1.4 cm (anterior) and 1.6 cm (posterior) (Anderson et al., 1974).

Milk yield averaged $59 \text{ g kg}^{-0.75} \text{ day}^{-1}$ in *O. h. columbianus* (Sadleir, 1980) and most of the milk was produced in the posterior quadrants (Mueller and Sadleir, 1977). Those authors noted that nutrient composition of deer milk increased with fawn growth. Milk of *O. h. columbianus* contained 1.4% ash, 5.4% lactose, 7.6% protein, and 10.9% fat (Jeness and Sloan, 1970). The relatively high fat, hence high energy levels ($1,650 \text{ kcal kg}^{-1}$), of deer milk (Short, 1981) may have survival value for the neonate because feeding can occur at relatively long intervals (Mueller and Sadleir, 1977).

In *O. h. hemionus*, total muscle and bone averaged 46.9% and 10.3%, respectively, of the carcass weight of four adults (Hakonson and Whicker, 1971a) and 34.5% and 17.7%, respectively, of the carcass weight of three fetuses (Hakonson and Whicker, 1971b).

Mule-deer-antler (pedicel) primordia were visible in both sexes 73 to 83 days after conception (Hudson and Browman, 1959). Growth of the male pedicel from the frontal bones began about 80 to 93 days from birth (Davis, 1962; Robinette et al., 1977). The fawn antler is typically skin-covered and consists of the pedicel and the base of the yearling antler beam (Cowan, 1936) ranging from about 3.5 to 8.0 cm in length in *O. h. hemionus* (Anderson and Medin, 1971). Occasionally, fawns about 5 to 7 months of age may have 1.0 to 2.5 cm of either hard antler or bony tips attached to skin-covered pedicels (Anderson and Medin, 1971). In the mature male, antler growth begins from the concave pedicel about 2 weeks (Linsdale and Tomich, 1953) to 2 months (Leopold et al., 1951) after antler shedding. Among races of *O. hemionus*, antler growth begins from about 23 February (Linsdale and Tomich, 1953) to 15 July (Swank, 1958) and terminates on 28 July (Linsdale and Tomich, 1953) to 22 October (Anderson and Medin, 1971).

The growing antler is covered with velvet, a modified extension of normal skin of the head and pedicels that is shed after growth ceases (Bubenik, 1966). The annual cycle of antler growth in *Odocoileus* is initiated and controlled by changes in day length acting on several cell types of the anterior pituitary (Nicolls, 1971). Hypothetically, those cell types secrete growth-stimulating hormones that act mainly on the antler and incidentally on the testes (Nicolls, 1971). Antler hardening, shedding, and the breeding period are mediated by decreasing day length through action of gonadotropins on Leydig cells, thus producing androgens (Goss, 1963, 1980; Markwald et al., 1971; Nicolls, 1971; West and Nordan, 1976). Androgens induce secondary ossification, accelerate maturation, induce behavioral changes to shed antler velvet, and aid in the maintenance of osteoblasts and osteocytes to maintain antlers in hard bone condition (West and Nordan, 1976). Withdrawal of androgens at the end of the breeding season permits resorption of bone at the pedicel-antler junction (Fig. 1) and antler shedding (West and Nordan, 1976). Extreme dates of antler shedding were from about 20 October (Robinette et al., 1977) to 20 April (Swank, 1958) and may encompass 16 weeks (17 December to 10 April) for individual populations (Anderson and Medin, 1971).

Costal cortical bone was mobilized during antler growth and replaced after growth while maintaining a constant skeletal bone mineral composition throughout the cycle (Banks et al., 1968a). This cyclic physiological osteoporosis occurred even though dietary intake of minerals was adequate (Banks et al., 1968a, 1968b; Hillman et al., 1973).

Completely ossified (mature) antler has a sheath 7 to 10 mm thick and a base of solid hard bone that extends to the external burr or corona. The sheath completely surrounds a core of spongy bone at its tip that grades into coarser spongy bone to the corona (Cowan, 1936; Modell, 1969).

Antler development in *Odocoileus* was related experimentally to nutritional levels (French et al., 1956) especially during the late-summer stage of antler growth (Long et al., 1959). Anderson and Medin (1969) reported strong positive correlations between various antler measurements and antler weight, eviscerated carcass weight and antler weight, and estimated age and antler weight.

All but 2 of 17 antlered deer reported as females had poorly

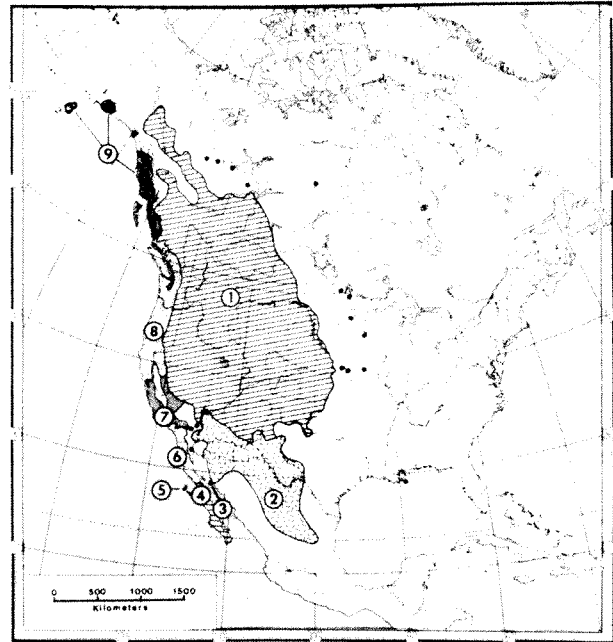


FIGURE 3. Distribution of *O. hemionus*. Lines enclose more or less continuously occupied range; outlying points are locations of specimens referenced by Hall (1981) where persistent populations do not occur; 1, *O. h. hemionus*; 2, *O. h. crooki*; 3, *O. h. sheldoni*; 4, *O. h. peninsulæ*; 5, *O. h. cerrosensis*; 6, *O. h. fuliginatus*; 7, *O. h. californicus*; 8, *O. h. columbianus*; 9, *O. h. sitkensis*.

developed antlers in velvet; six were with fawns, had fetuses, or were lactating, but antlers were known to be deciduous in only one individual (Anderson, 1981). The latter female bore fawns, had a normal karyotype, and histologically normal endocrine glands (Mierau, 1972).

Mule deer have heterodont and brachyodont dentition whose histologic development resembles that in other mammals (Rees et al., 1966a). The permanent dental formula for the genus *Odocoileus* is: i 0/3, c 0/1, p 3/3, m 3/3, total 32.

Hudson and Browman (1959) and Short (1970) noted that enamel tips of incisors were visible at about 161 days and were erupted partially approximately 180 days from conception. Lower incisors and canines were erupted fully among seven 10-day-old mule deer fawns. The second, third, and fourth deciduous premolars were erupted fully and mineralized at about 2.5 to 3 months of age (Rees et al., 1966b). Eruption and formation of the teeth of *O. h. hemionus* were complete at about 29 months (Rees et al., 1966b). Although unreliable, subjective estimates of the relative wear of the molariform teeth and the chronology of tooth replacement were used extensively to estimate ages of mule deer (Brown, 1961; Erickson et al., 1970; Robinette et al., 1957b; Taber and Dasmann, 1958; Thomas and Bandy, 1975).

Completely accurate age estimates were obtained from small samples of mule deer of known age by counting cementum annuli in the root of the first permanent incisor (Erickson and Seliger, 1969; Low and Cowan, 1963). However, the cementum-annuli technique also is somewhat subjective, and subsequent tests with 55 *O. virginianus* (Sauer, 1971) and 49 *O. h. hemionus* (Robinette et al., 1977) of known age revealed errors of 16% and 51%, respectively.

Ranges of mean values of selected cellular constituents of *O. hemionus* blood from several studies were: hemoglobin, 9.8 to 20.5 g/100 ml; packed cell volume, 30.6 to 58.2%; erythrocytes, 4.6 to 14.2 $10^6/\text{mm}^3$; and leukocytes, 3.0 to 5.8 $10^3/\text{mm}^3$ (Anderson, 1981). Similar values for selected serum constituents of *O. hemionus* were: total protein, 4.6 to 8.5 g/100 ml; blood urea nitrogen, 7.4 to 29.8 mg/100 ml; inorganic phosphorus, 5.2 to 11.2 mg/100 ml; and vitamin A, 151.9 to 367.7 IU (Anderson 1981).

In mature *O. h. hemionus*, mean (\pm SE) fresh brain weights (in grams) for 50 males and 89 females were 197.7 ± 2.7 and 189.3 ± 1.8 , respectively. Similar values for the right lung of 37

male and 62 females were 772.8 ± 50.6 and 636.6 ± 21.2 , respectively, and for the left lung of 38 males and 62 females 479.5 ± 28.0 and 408.5 ± 12.0 , respectively (Anderson et al., 1974).

The stomach of fawns less than 5 weeks old is monogastric and consists of the abomasum, an efficient organ for utilizing milk (Short, 1981). Over the next 11 weeks the digestive system develops into a highly specialized, four-compartment ruminant stomach with the same relative volume, functions, and appearance of that of adult deer (Short, 1981). The large and small intestines of *O. hemionus* are about 5 and 15 m in length, respectively (Short, 1981). The stomach of mule deer is relatively small compared with that of other ruminants (Short et al., 1965). Foods are often retained in the rumen of mule deer for less than 1 day (Short, 1981). During late spring, summer, and autumn, rapid rates of food consumption and passage of easily digestible foods through the gastrointestinal tract produce abundant assimilable nutrients in contrast with diminished levels in late autumn and winter (Short, 1981). Bacterial populations in the rumen of *O. h. hemionus* averaged about 11 billion and 12 billion per ml of rumen fluid during spring and late autumn and winter, respectively (Pearson, 1969).

In general, various carcass fat indices increased during maximum food intake in summer, and peaked during autumn just before the breeding period, decreased precipitously during the breeding period, and continued to decline until spring (Anderson et al., 1972; Short, 1981). Females generally lagged about 1 to 2 months behind males in the annual fat cycle (Anderson et al., 1972). Predicted annual weight losses for 5-year-old *O. h. hemionus* approximated 19% of the peak weight of males and 22% of the peak weight of females (Anderson et al., 1974). For deer, fat probably functions primarily as a store of energy for survival; the insulative subcutaneous fat layer essentially was depleted by early winter (Anderson et al., 1972).

Mule deer have excellent binocular (Cowan, 1956a) and probably color vision (Scott, 1981; Witzel et al., 1978). Apparently they usually are unable to detect motionless objects but are extraordinarily sensitive to movement. The sense of hearing is extremely acute (Cowan, 1956a; Moen, 1973).

The mean and range (in parentheses) of body core temperatures ($^{\circ}\text{C}$) of *O. h. hemionus* were 37.1 (36.3 to 42.1) for a semitame, captive, undisturbed yearling male (Thorne, 1975), and 38.9 (38.4 to 39.8) for two male fawns and 38.3 (37.8 to 39.3) for two adult female *O. h. columbianus* in captivity (Cowan and Wood, 1955).

Mean water intake (ml/kg body mass) of confined deer was 51 (Bissell et al., 1955): 24 to 35 in winter and 47 to 70 in summer (Nichol, 1938) for mule deer and 53 in winter and 104 in summer (Longhurst et al., 1970) for *O. h. columbianus*. Seasonal variations in water intake and forage intake are correlated (Short, 1981). Seasonally, free water may not be necessary in some habitats; wintering deer in temperate zones may meet their water requirements by eating snow (Cowan, 1956a). *O. h. crooki* may do so by eating cacti and other succulents (Short, 1977).

Daily mean defecation rates in *Odocoileus* from 24 studies ranged from 8.0 to 23.1 fecal pellet groups per deer; 12.0 to 13.0 groups per day were reported most frequently (Neff, 1968). High forage intake, high moisture content, high proportion of young in population, change from roughage to concentrated diets, and captivity were associated with high defecation rates (Neff, 1968). In spite of the variation, Neff (1968:597) reported "reasonable accuracy of estimate" of density of deer populations in enclosures with known numbers of deer by counts of groups of fecal pellets.

ONTOGENY AND REPRODUCTION. Most wild *O. hemionus* females conceive during their second year and only rarely during their first year (Nellis et al., 1976; Thomas and Smith, 1973) but up to 50% of captive *O. h. columbianus* fawns conceived in their first year (Mueller and Sadleir, 1979). Based on 23 studies, breeding records for the species extend from about 12 September to 7 March. The breeding peak in mule deer occurs mainly from late November through mid-December and during late November in black-tailed deer (Anderson, 1981).

Counts of corpora lutea exceeded counts of fetuses in 6 of 907 pregnant does indicating either monozygotic twinning or polyovular follicles. Determination of sex was possible for three of the six sets of twins; each pair was of the same sex suggesting monozygotic twinning (Robinette et al., 1977). Brown (1961) and Illige

and Erling (1955) reported similar instances in one *O. h. columbianus* and one *O. h. crooki*, respectively.

Mean gestation lengths for *O. hemionus* approximated 200 to 208 days with a range of 183 to 218 days based on 65 deer from five sets of data (Anderson, 1981). Fetal growth curves of *O. h. hemionus* were depicted qualitatively based on forehead-rump length of prenatal young of known age (Hudson and Browman, 1959) and quantitatively based on body mass of prenatal young of known age (Robinette et al., 1977). Length of forehead-rump and hindfoot were correlated more strongly with duration of gestation than with body mass in 21 *O. virginianus* fetuses with known dates of conception (Short, 1970).

Peak birth periods in *O. h. hemionus* were estimated as 19 to 20 June (Robinette et al., 1977) and 16 June to 6 July (Anderson and Medin, 1967). Extreme birth dates in that race were 16 May to early October et al., 1977). Most *O. h. columbianus* were born in June (Thomas and Cowan, 1975). Variation was associated partly with the diverse environments and phenology represented. For example, Robinette et al. (1977) calculated that a 305-m rise in elevation was associated with a 7-day delay in the birth period. Mean mass at birth for *O. h. hemionus* in six studies ($n = 358$) ranged from 2.74 to 3.99 kg with extremes of 2.27 to 5.00 kg. Similar values for *O. h. columbianus* in four studies ($n = 79$) were 2.97 to 3.29 kg and 2.04 to 4.54 kg (Anderson, 1981). Average mass at birth was affected by litter size and sex; singles averaged heavier than twins and, in sets of twins of opposite sex, males averaged heavier (Robinette et al., 1977). Malnutrition of dams reduced fetal weights and birth weights (Verme, 1963).

Average fetuses per doe for *O. hemionus* from 25 studies totaling 1,795 females ranged from 1.14 to 1.85 for all does examined and 1.43 to 1.89 per pregnant doe (Anderson, 1981). Mean numbers of fetuses per doe vary with nutritional levels (Robinette et al., 1973). The common litter size is two, with deer in their first or second breeding year most frequently producing singletons. Triplets occurred in 1.4% and quadruplets in 0.07% of the total examined; these were, with one exception, limited to *O. h. hemionus*. A preponderance of male fetuses are produced in most *O. hemionus* populations: 111:100, based on 2,299 fetuses from several western states (Robinette et al., 1957a). In *Odocoileus*, male neonates may predominate when poor nutrition prevails about 6 weeks before, and during, the breeding period (Verme, 1969), or when delayed breeding occurs (Verme and Ozoga, 1981).

Sperm production, serum testosterone, and testicular volume in both wild and captive *O. h. columbianus* were greatest during November and lowest in February and March, although sperm quality appeared adequate for successful breeding from September through January (West and Nordan, 1976). In *O. h. hemionus*, testicular mass and volume also were maximal during November but minimal during April-May; maximum size decreased with age following age 7 years (Anderson et al., 1974).

A mean daily gain of 0.22 kg for males and 0.21 kg for females was estimated from growth-in-weight curves for *O. h. hemionus* twins from birth to 150 days of age (Robinette et al., 1973). Based on 10 studies, gross estimates of gain in body mass for deer less than 1 year of age averaged 0.09 to 0.50 kg/day for *O. h. hemionus* and 0.05 to 0.27 kg/day for *O. h. columbianus* (Anderson, 1981).

Weaning begins at about 5 weeks of age and usually is completed at age 16 weeks (Short, 1981). However, deer were observed to nurse at about 32 (Mueller and Sadleir, 1977) and 36 to 56 weeks of age (Hanson, 1958).

In *O. h. hemionus*, full development of most skeletal attributes occurred at about age 49 months (male) and 37 months (female) (Anderson et al., 1974). However, predicted gains in carcass mass were continuous to about age 120 months for males and 96 months for females (Anderson et al., 1974).

Thomas and Cowan (1975:261) found that wild *O. h. columbianus* first ovulated in November but did not become pregnant "... even though some ova were penetrated by spermatozoa and began to cleave." The second ovulation occurred 8 to 9 days later during which 97% of 61 females conceived. During the second ovulation, about half of the does ovulated in a span of 7 to 8 days and most late ovulators were yearlings. Estrus occurred every third follicular cycle of 8 to 9 days in length. The length of the estrous cycle for confined *O. h. columbianus* thus was calculated as 23 to 29 days. As many as five periods of estrus may occur when does repeatedly fail to conceive. The period of estrus was 24 to 36 h in

captive *O. h. columbianus* (West, 1968). Ovulation in *Odocoileus* occurs about 12 to 14 h after estrus terminates (Verme and Ozoga, 1981). About 27 to 29 days elapsed between conception and implantation in *O. h. hemionus* (Hudson and Browman, 1959). Corpora lutea of pregnancy developed into corpora albicantia that equaled the number of implanted embryos and persisted for the life of the doe (Thomas and Cowan, 1975).

As estimated by the difference between counts of corpora lutea of pregnancy and of fetuses, losses of ova in *O. hemionus* ranged from 3.4 (Thomas, 1970) to 10.5% (Robinette et al., 1955). Annual rates of postnatal mortality among five "stable" *O. hemionus* populations ranged from 22 to 53% for males, 17 to 25% for females, and 45 to 69% for fawns of each sex (Connolly, 1981a).

Average longevity of *O. hemionus* has not been documented. Maximum longevity in the wild was 19 years for a male (Robinette et al., 1977) and 20 years for a female (Ross, 1934). A semi-captive female *O. h. columbianus* reached 22 years of age (Cowan, 1956b).

ECOLOGY. Optimum growth and productivity of individuals and populations are dependent upon adequate supplies of highly digestible, succulent forage (Robinette et al., 1973; Short, 1981). Diets consisting primarily of woody twigs cannot meet maintenance requirements of deer (Wallmo et al., 1977). Summaries of deer diets by Kufeld et al. (1973) and Longhurst et al. (1979) and several authors in Wallmo (1981b) show that the traditional characterization of these deer as "browsers," in the sense of subsisting mostly on woody forage, is inaccurate. Based on its stomach structure and its diet of woody and herbaceous forage in approximate equal proportions, *O. hemionus* is classified more aptly as an "intermediate feeder" (Hofmann and Stewart, 1972).

Because nutritious forage is in poor supply for much of the year, theoretically both *Odocoileus hemionus* and *O. virginianus* have an annual cycle of metabolic rates (Nordan et al., 1970; Silver et al., 1969) in which higher energy flux and food intake in summer (French et al., 1956; Nordan et al., 1970; Wood et al., 1962) enables deer to capitalize on abundant high-quality forage for growth, production, and fat storage. A lower energy flux in winter permits them to survive lower intake of poor-quality forage while minimizing the catabolism of stored fat for body functions. Although evidence for annual cycle is based primarily on experiments with tame animals, Anderson et al. (1974) demonstrated periodicity in growth and fat deposits in a wild population of *O. h. hemionus* in Colorado.

Estimated rate of food intake was about 22 g (air-dry basis) $\text{kg}^{-1} \text{day}^{-1}$ (Aldredge et al., 1974; Nichol, 1938), equivalent to 1.5 kg of air-dry forage per day for a 68-kg deer. Fawns appear to consume more per unit of body mass year-round (ca 31 to 38 g/kg) and adults less in winter (ca 17 g/kg) (Aldredge et al., 1974). In adult males, food intake drops abruptly with onset of rut (Bandy et al., 1970; Nordan et al., 1970). Mean intake of dry matter for nonlactating black-tailed deer females was 67 g $\text{kg}^{-0.75} \text{day}^{-1}$ that furnished 247 kcal digestible energy $\text{kg}^{-0.75} \text{day}^{-1}$. Lactating females with singletons and twins consumed 135% and 170%, respectively, of the intake of nonlactating females (Sadleir, 1982). About 158 kcal digestible energy/ $\text{kg}^{-0.75} \text{day}^{-1}$ is the maintenance requirement for mule deer fawns during winter (Baker et al., 1979). Kautz et al. (1981) estimated composite winter energy expenditures while bedded, standing, walking, and trotting of three tame fawn mule deer as 94 to 446 kcal $\text{kg}^{-0.75} \text{day}^{-1}$. Heart rates of those deer ranged from 46 to 96 beats/min and were significantly ($P < 0.001$) correlated ($r = 0.69$) with energy expenditures.

Individuals of *O. hemionus* tend to confine their daily movements to discrete "home ranges." Where seasonally migratory, most deer with established home ranges use approximately the same winter and summer home ranges in consecutive years (Bertram and Rempel, 1977; Carpenter et al., 1979; Gruell and Papez, 1963; Robinette, 1966; Robinette et al., 1977; Zalunardo, 1965). Harestad and Bunnell (1979) calculated mean size of the annual home range from several studies as 58.8 ha ($n = 81$) for *O. h. columbianus* and 285.3 ha ($n = 110$) for *O. h. hemionus* and showed that male *Odocoileus* have larger home ranges. Other estimates of the size of annual mean home ranges ranged from 39 ha for yearling female *O. h. columbianus* in Oregon coastal forest (Miller, 1970) to 3,379 ha for adult female *O. h. hemionus* on the Great Plains (Severson and Carter, 1978). Variation in estimates of mean home range size of *O. hemionus* probably is associated with interactions

among sex, age, body mass, season, race, habitat, and method of computing home range size.

According to Dasmann and Taber (1956), a nonmigratory population of *O. h. columbianus* exhibited three types of movements outside the home range: breeding season travels, wandering, and dispersal. Bunnell and Harestad (1983:201) defined dispersal as "... individual movements out of an area larger than a home range that exhibit no predictable return." Movements of *O. h. columbianus* greater than 5 km were dispersive and averaged 15.2 and 12.2 km for males and females, respectively (Bunnell and Harestad, 1983). Male, but not female, dispersal increased with increases in density (Bunnell and Harestad, 1983). Robinette (1966) and Severson and Carter (1978) defined dispersal in *O. h. hemionus* as movements beyond the home range to distances of 1.6 km and 8.0 km, respectively, that resulted in establishment of a new home range. Male *O. h. hemionus* tagged as fawns dispersed (air line distances) from 97 to 217 km (Robinette, 1966), and a female *O. h. hemionus* moved 180 km (Severson and Carter, 1978). In one migratory population of that race, few deer dispersed as fawns but 60% of the yearling bucks and 35% of the yearling does apparently dispersed by 16 months of age (Robinette, 1966).

Seasonal movements exceeding about 15 km or involving migrations from higher elevations (summer ranges) to lower winter ranges are associated, in part, with decreasing temperatures, severe snowstorms, and snow depths that reduce mobility and food supply (Leopold et al., 1951; Russell, 1932). On the winter range, snow depths in excess of 25 to 30 cm impede movement (Loveless, 1967) and excess of 51 to 60 cm discourage continuous occupation (Gilbert et al., 1970; Loveless, 1967). Thus, deep snows ultimately limit useable range to a fraction of the total. The chronology of spring movement from lower (winter ranges) to upper (summer ranges) elevations presumably is an interaction of plant phenology, rate of snow melt, and, perhaps, impending birth period (Russell, 1932). Mule deer in the arid southwest may migrate in response to rainfall patterns (Longhurst and Chaitin, 1941). Autumn and spring migrations may encompass 4 weeks in *O. h. hemionus* (Wright and Swift, 1942) or 6 or 7 weeks with delays enroute of about 40 days in *O. h. californicus*; individual deer appeared to follow the same route for both autumn and spring migrations (Bertram and Rempel, 1977). Migratory routes may (Leopold et al., 1951; Russell, 1932), or may not (Gruell and Papez, 1963; Bertram and Rempel, 1977) be confined to major drainages or ridgetops, and may cross other winter ranges enroute to traditional wintering areas (Gruell and Papez, 1963; Jensen, 1968). Air line distances between summer and winter ranges traveled by individual, marked, migrating *O. h. hemionus* varied greatly within and among herds; means and ranges of distances reported (km) were 29.8 (0.4 to 129) (Zalunardo, 1965) and 15.4 (1.6 to 241) (Jensen, 1968).

Some measured posthunting densities (mean number of deer/ km^2) of migratory *O. h. hemionus* on winter ranges were 10.0 (Kufeld et al., 1980), and 16.0 (Robinette et al., 1977). In migratory populations of this race, a variable and unmeasured proportion of deer may be permanent residents on winter ranges. Densities of nonmigratory *O. h. hemionus* were estimated at 3.9/ km^2 during winter in prairie-woodland riverbreaks in Montana (Mackie, 1970). Densities of nonmigratory *O. h. columbianus* were estimated on relatively small areas as 18.5 deer/ km^2 in forest habitat (Brown, 1961), and 49.8/ km^2 (Longhurst et al., 1979) and 21.2 to 55.6 deer/ km^2 (Dasmann and Taber, 1956) in chaparral habitat.

Common predators of mule deer include pumas, *Felis concolor*; coyotes, *Canis latrans*; bobcats, *Felis rufus*; golden eagles, *Aquila chrysaetos*; domestic and feral dogs, *Canis familiaris*; and black bears, *Ursus americanus* (Connolly, 1981b).

Sources of mortality other than predation probably are more effective regulators of population density; at least, they are measured more easily. For example, legal hunting from 1950 to 1975 accounted for an estimated 1.73 million mule deer and 33,000 black-tailed deer on U.S. National Forests alone. No reliable estimates are available for the total kill of *O. hemionus* in the U.S. (Connolly, 1981c), Mexico, and Canada.

Additional unrecorded mortality associated with hunting includes "cripple-kills" (wounded deer that die), deer killed legally and abandoned by hunters, and illegal kills. Among five intensive field surveys, estimates of crippling loss plus illegal kills ranged from 8 to 92% of the estimated legal kill and were greater where a buck-only hunting regulation was in effect (Connolly, 1981a). Connolly (1981b) generalized that hunting can regulate local populations but

not cause general declines over large areas; hunting bucks may increase deer numbers, and hunting does may reduce deer numbers in proportion to the percentage of does killed annually.

Diseases and parasites of *O. hemionus* listed and discussed by Hibler (1981) include: viral—bluetongue; epizootic hemorrhagic disease; foot-and-mouth disease; malignant catarrhal fever; bovine virus diarrhea/mucosal complex; neoplastic (non-malignant papillomas and fibromas); bacterial—pasteurellosis, *Pasteurella multocida*; brucellosis, *Brucella* spp.; necrobacillosis, *Fusibacterium necrophorum*; actinomycosis, *Actinomyces bovis*; blackleg and malignant edema, *Clostridium chauvei* and *Cl. septicum*; caseous lymphadenitis, *Corynebacterium ovis* and *C. pyogenes*; anthrax, *Bacillus anthracis*; parasitic—elaeophorosis, *Elaeophora schneideri*; setaria, *Setaria yehi*; parelaphostrongylosis, *Parelaphostrongylus tenuis*; gastrointestinal parasitism by nematodes of the genera *Haemonchus*, *Ostertagia*, *Trichostrongylus*, *Nematodirus*, *Nematodierella*, *Trichuris*, *Capillaria*; lungworms, *Dictyocaulus* spp., *Protostrongylus macrotis*, *Parelaphostrongylus odocoilei*; foot worm, *Onchocerca cervipedis*; eye worm, *Thelazia californiensis*; tape-worms (larval stages of *Taenia hydatigena*, *T. krabbei* and adult *Moneizia* spp., *Thysanosoma actinioides*, *Echinococcus granulosus*); liver flukes, *Fasciola hepatica* and *Fascioloides magna*; sarcocystis, *Sarcocystis* spp.; toxoplasmosis, *Toxoplasma gondii*; myiasis, *Cephenemyia jellisoni*, *C. apicata*; bloodsucking diptera of the genera *Hybomitra*, *Tabanus* spp., *Simulium* spp., *Symphomyia*, *Chrysops* spp., *Aedes*, *Culex*, *Culiseta*, *Leptoconops*; louse flies, *Lipoptena depressa*, *Neolipoptena ferrisi*; native lice of the genera *Haematopinus*, *Linognathus*, *Tricholipeuris*, *Cervophthirus*; fleas, *Pulex irritans*; ticks, *Otobius megnini*, *Dermacentor albipictus*, *D. andersoni*, *Ixodes scapularis*, *I. pacificus*, *Ornithodoros coriaceus*; and anaplasmosis, *Anaplasma marginale*. Hibler (1981) noted that an infectious or parasitic disease could be a primary mortality factor or the result of a predisposing factor. For example, heavy burdens of gastrointestinal nematodes may cause death, but usually are indicative of such predisposing factors as high deer densities and malnutrition. Livestock may transmit diseases to deer as in the foot-and-mouth disease epidemic in California in 1924 where over 22,000 deer were killed to control the disease (Hibler, 1981). Conversely, deer frequently are latent carriers of anaplasmosis, a disease often fatal to livestock. Infections of meningeal worm, *Parelaphostrongylus tenuis*, are tolerated by *O. virginianus* but may cause fatal neurologic disease in *O. hemionus* and other cervids where their natural or introduced ranges overlap (Hibler, 1981).

Anomalies of *O. hemionus* include sickle cell (Dougherty, 1939), brachygnathism (Short, 1964), retracted leg tendons, bowed leg bones, curved spine, cleft palate in fawns (Hines, 1975), stomach calculi (Draney and Robinette, 1955), vestigial first digit, splayed front hooves, two maxillary canines, two p1 (premolars), missing p2, and uterine eversion (Robinette et al., 1977).

The adequacy of "cover" and the degree of competition with other herbivores for forage, particularly domestic livestock, often are considered actual or potential regulators of density in *O. hemionus* populations. So far, cover requirements are hypothetical but not demonstrated (Moen, 1973; Thomas, 1979). The literature on the effects of range competition (Mackie, 1981) reveals only that they are understood poorly.

BEHAVIOR. *Odocoileus hemionus* is polygynous and, although Robinette et al. (1977:71) refer to harems in *O. h. hemionus*, the breeding system is generally regarded as the tending-bond type (Geist, 1981). Thus, courtship and mating occur within the group; the dominant buck tends an estrous doe until mating or displacement by another buck occurs (Kucera, 1978). Among *O. h. columbianus*, only the dominant buck exhibited territorialism during the breeding period (Miller, 1974). Dominance was largely a function of size; the largest bucks with the largest antlers performed most of the copulations (Kucera, 1978; Miller, 1974). Frequency of heterosexual behavior was strongly and positively correlated with antler size in *O. h. crooki* (Kucera, 1978). Serious fights were rare and limited to large bucks (Kucera, 1978; Wachtel et al., 1978).

The social system consists of "female clans related by maternal descent that are facultative resource defenders and bucks dispersed as individuals or in groups of unrelated individuals" (Geist 1981:213). During winter and spring, the stability of close-family and buck groups was maintained in *O. h. columbianus* with domi-

nance hierarchies (Miller, 1974). Increases in strife and alarm behavior and decreases in play among fawns occurred as population density increased (Dasmann and Taber, 1957; Miller, 1974). Pregnant and maternal does exhibited mutual intolerance and strong spatial regulation but bucks did not (Dasmann and Taber, 1956). Frequency of aggressive behavior between sexes remained low year-long in *O. h. californicus* (Koutnik, 1981).

Communication among *O. h. hemionus* is facilitated by the sebaceous and sudoriferous secretory cells of five integumentary glands. The cells of each gland produce specific scents (pheromones) that release specific reactions of conspecifics (Müller-Schwarze, 1971; Müller-Schwarze and Müller-Schwarze, 1975). The metatarsal (outer surface of each hindfoot) acts as an alarm pheromone, the tarsal (inner surface of each hock) aids in mutual recognition, the interdigital may leave a scent trail, and the function of the tail gland is uncertain (Müller-Schwarze, 1971). The pheromone from the forehead skin, in combination with the pheromone from the antorbital sac (anterior to the eye), may signal the home range of individual deer (Müller-Schwarze, 1971) or the presence of individual male deer (Volkman et al., 1978). Urine has a pheromone function at all ages and by both sexes (Müller-Schwarze, 1969); it is deposited on tufts of hair surrounding tarsal glands when the tufts are rubbed together (Müller-Schwarze et al., 1978; Geist, 1981). "Rub-urinating" may signal distress in fawns but threat in adults (Müller-Schwarze, 1971) and is a major dominance display of mule deer (Geist, 1981).

GENETICS. The diploid number in *O. hemionus* is 70. Autosomes are two submetacentrics and 66 acrocentrics or telocentrics. Sex chromosomes are a submetacentric X and a metacentric Y (Hsu and Benirschke, 1967).

Wild hybrid *O. hemionus* and *O. virginianus* were described (Cowan, 1962; Wishart, 1980), but those authors and Day (1980), Hoffmeister (1962), and Kramer (1973), believed such hybrids were rare. Hybrids are produced easily in captivity, but their survival (particularly fawns) is poor (Day, 1980; Nichol, 1938). Day (1980) reported that mature male and female F₁ hybrids were both fertile but two F₁ crosses were not successful. Wishart (1980) speculated that, in the wild, introgressive hybridization and eventual loss of *O. virginianus* characters are probable. Intergradation of *O. h. hemionus* and *O. h. columbianus* occurs in northeastern California and southern British Columbia (Cowan, 1936) and Oregon (Wallmo, 1981a). Little effort has been made to discriminate between phenotypic and genotypic variation among subspecies (Wallmo, 1981a). Melanism and albinism, including a true albino, were recorded for *O. h. hemionus* (Robinette et al., 1977).

REMARKS. We have followed usage of the generic name *Odocoileus* rather than *Dama* (Hall, 1981) because of opinion 581 of the International Commission on Zoological Nomenclature (Jones et al., 1982).

We thank Gwen A. Anderson who made the drawings; Geoffrey Tischbein for the photograph; Marian Hershcopf for assisting in the literature search; Jann Black, Nancy McEwen, and Karen Wilken for manuscript preparation; and Robert B. Finley, Jr., for loan of skulls in his care.

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