Antilocapra americana. By Bart W. O'Gara

Antilocapra Ord, 1818

Antilocapra Ord, 1818:149. Type species *Antilope americanus* Ord, 1815.
Dicranocerus Hamilton-Smith *in* Griffith, 1827:169, as a subgenus of *Antilope*. Type species *A. furcifer* Hamilton-Smith.

CONTEXT AND CONTENT. Order Artiodactyla, Suborder Ruminantia, Infraorder Pecora, Family Bovidae, Subfamily Antilocaprinae, Tribe Antilocaprini. The genus *Antilocapra* has one species.

Antilocapra americana (Ord, 1815)
Pronghorn

Antilope americanus Ord, 1815:292. Type locality, plains and highlands of Missouri River.
Antilocapra americana, Ord, 1818:149.
Antilope (Dicranocerus) Furcifer Hamilton-Smith, 1827:170, a renaming of Ord's *americanus*.
Antilocapra anteflexa Gray, 1855:10. Type locality "most probably from America."

CONTEXT AND CONTENT. Context noted in generic summary. Five subspecies are generally recognized:

A. a. americana (Ord, 1815:292), see above (*anteflexa* Gray a synonym).
A. a. mexicana Merriam, 1901:31. Type locality "Sierra en media, Chihuahua, Mexico."
A. a. peninsularis Nelson, 1912:107. Type locality "45 miles south of Calmalli, Lower California, Mexico."
A. a. oregona Bailey, 1932:45. Type locality "Hart Mountain (Mount Warner) Oregon."
A. a. sonoriensis Goldman, 1945:3. Type locality "40 miles north of Costa Rica, a ranch on the northern side of the Rio De Sonora, southwest of Hermosillo, Sonora, Mexico."

DIAGNOSIS. Because the genus includes only one species, the following diagnosis applies both to the genus and species. Two rump patches of white erectile hair, approximately 75 mm long, are visible at great distances. Horns of males and females are supraorbital; cores osseous and cancellated (Murie, 1870). Horns of males are dark colored with whitish tips and anterior prongs, the tips are variable but normally incline inward or backward, or both; horn sheaths of adult males range from 33 to 50 cm and are shed annually a month or more after the rut; unbranched horn cores range from 12 to 15 cm in length, are compressed laterally, and are somewhat triangular in cross section; horn sheaths are present or absent on females, seldom exceed 12 cm in length, and seldom bear prongs; hornless females have horn cores about 3 mm long under whorls of hair; horned females generally have horn cores from 12 to 76 mm long and round to oval in cross section; horn sheaths of females are deciduous but the time of shedding is variable (O'Gara, 1969b).

GENERAL CHARACTERS. Average body measurements (mm) of adult females and adult males collected in Alberta (Mitchell, 1971) are: total length 1406, 1415; height at shoulder 860, 875; length of tail 97, 105; and length of ear 142, 143. Measurements available from other subspecies fall within the ranges of measurements reported for *A. a. americana*. Weights vary seasonally, adult *A. a. americana* does collected throughout the year in Alberta averaged 50 kg and ranged from 47 to 56 kg; males in the same collection averaged 57 kg and ranged from 47 to 70 kg (Mitchell, 1971); adult *A. a. mexicana* does and bucks in Texas averaged 40 and 41 kg (Buechner, 1950). Build is rather robust; legs and feet are relatively long and slender; feet lack lateral digits. Head and eyes are large; eyes are black, protected from mechanical damage by tubular bony orbits, and from sun by heavy black eyelashes. Body colors are contrasting white and rusty brown to tan, and black and dark brown markings occur about the head and neck. The eyelashes and mucous membranes of the nose and mouth are coal black, and brownish-black patches
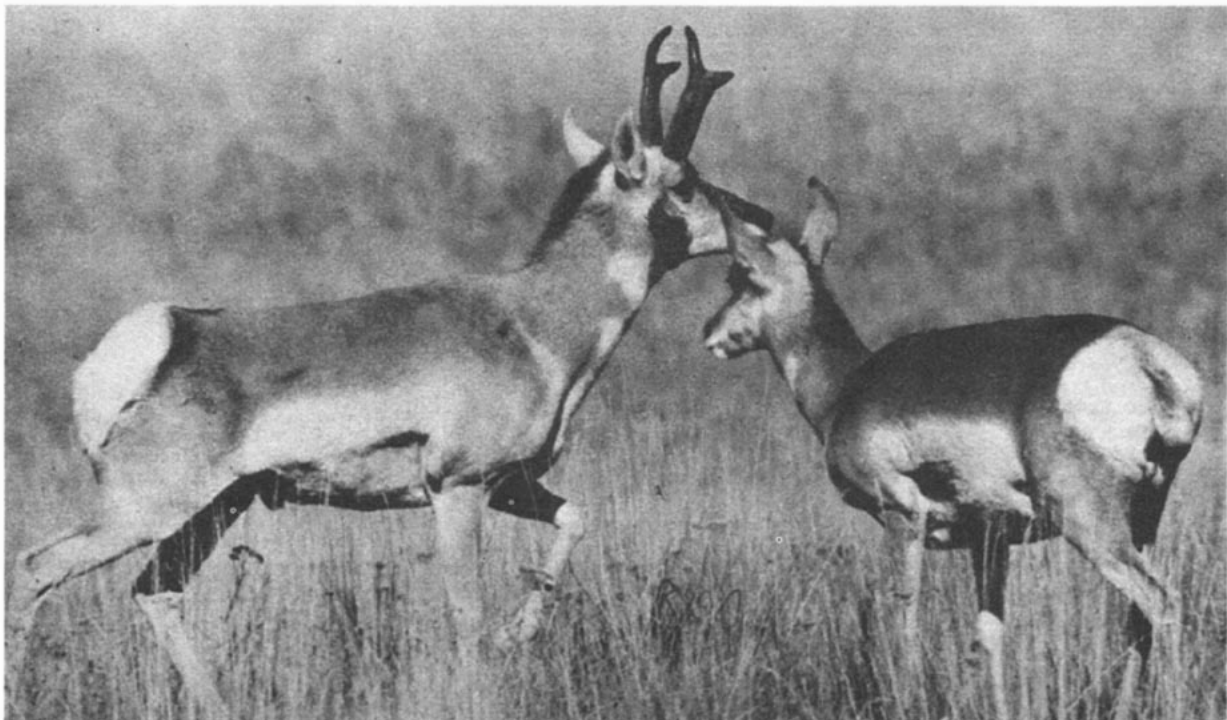

FIGURE 1. With prancing gait and waving head a courting buck presents his cheek patch to a doe. Photograph by author.
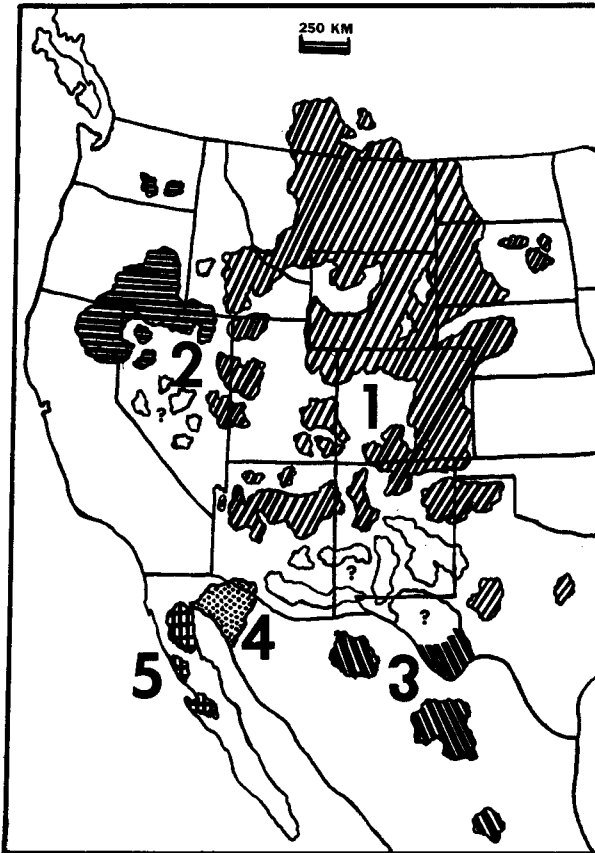
FIGURE 2. Present distribution of the subspecies of *Antilocapra americana*: 1, *A. a. americana*; 2, *A. a. oregona*; 3, *A. a. mexicana*; 4, *A. a. sonoriensis*; and 5, *A. a. peninsularis*.

start just below the ears of males and extend downward for 75 to 100 mm. Erectile hairs of mane, 70 to 100 mm in length, are russet and tipped with varying amounts of black. Southern races, except *A. a. peninsularis*, are paler in color than are northern races.

DISTRIBUTION. *A. a. americana.*—Formerly north to a little beyond the South Saskatchewan River in Saskatchewan, Red Deer River in Alberta, and southwestern Manitoba, Canada; southward to southern Texas, central New Mexico, central Arizona, and Colorado Desert of southern California; eastward to western Minnesota, western Iowa, northwestern Missouri, Kansas, and Oklahoma; and westward to western Montana, southern Idaho, Nevada, and California. *A. a. mexicana.*—Formerly southeastern Arizona, and southwestern New Mexico eastward to Jornada and Tularosa Desert valleys and region west of Organ Mountains, southward through extreme western Texas, Chihuahua, and Coahuila to northeastern Durango. *A. a. peninsularis.*—Central Baja California, south to head of Bolenas Bay in about lat. 27°N, and north on west coast to about lat. 29° 30′N; on gulf side to beyond lat. 32°N, to southern end of Colorado Desert. *A. a. oregona.*—Open sagebrush country of eastern Oregon; limits of range not determined. *A. a. sonoriensis.*—Desert plains of central and western Sonora, north to southern Arizona (Miller and Kellogg, 1955).

Lines of demarcation between the range of *A. a. americana* and those of *A. a. mexicana* and *A. a. oregona* (in figure 2) are uncertain. Buechner (1950) considered pronghorns west of the Pecos River in western Texas to be *A. a. mexicana* but thought intergrades with *A. a. americana* were common. More than 4000 pronghorns were transplanted in New Mexico between 1936 and 1957 (Russell, 1964) so subspecies are thoroughly mixed there. All the herds in southern Arizona that occur in grasslands have received transplants from northern Arizona; the desert populations on the Cabeza Prieta Game Range (*A. a. sonoriensis*) and at lake Havasu City (questionably *A. a. mexicana*) are the only herds in southern areas that have not received transplants (Kent Jackson, Arizona Fish and Game Department, personal communication). Hall (1946) considered the pronghorns of Nevada to be *A. a. americana* despite their close proximity to the type locality of *A. a. oregona*. Pronghorns in Washington State were transplanted from Oregon and the Charles Sheldon National Antelope Refuge in Nevada.
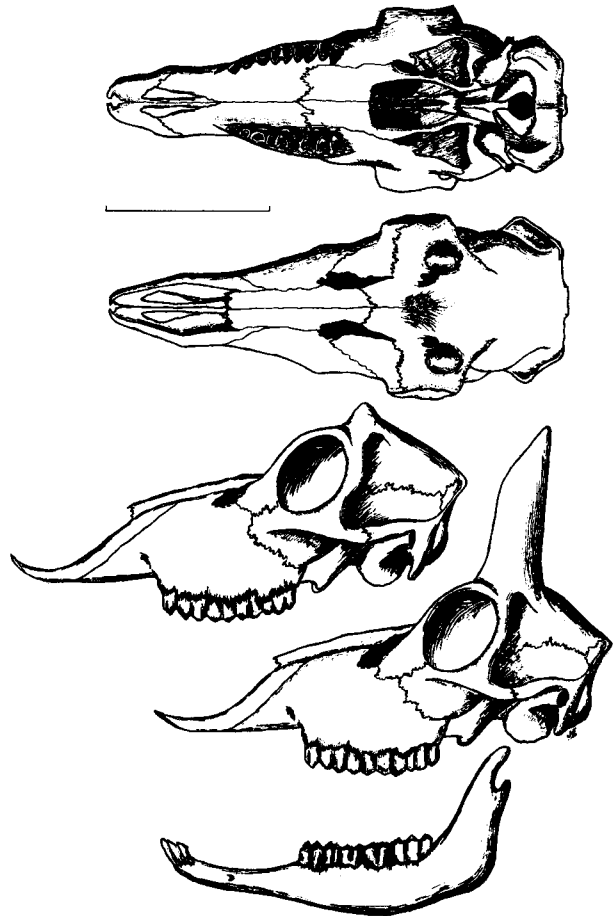

FIGURE 3. Views of skulls from female (top three) and male (bottom) *Antilocapra americana americana*. Line showing scale equals 100 mm. Sketched by John Eiler.

FOSSIL RECORD. Three genera of antilocaprines (Tribe Merycodontini) occurred during the Miocene. Fossil evidence regarding precursors to Merycodontini is lacking, but skeletal and dental characteristics support Matthew's (1934) contention that antilocaprines diverged early from a primitive bovid stock. While merycodonts possessed teeth and skeletons similar to, but somewhat more primitive than, those of *Antilocapra*, the horns appear to have been antlerlike and covered with skin. Approximately 4000 specimens of Merycodontini have been found, all within the historical range of *A. americana* (Frick, 1937). Thirteen now extinct genera of Antilocaprini occurred during the Pliocene and Pleistocene, mostly within the historic range of *A. americana*; however, one extinct genus (*Hexameryx*) and an extinct subgenus of *Antilocapra* (*Subantilocapra*) occurred in Florida during the middle Pliocene (Webb, 1973). The teeth and skeletons of the extinct genera of Antilocaprini were similar to those of *A. americana* and the horn cores, though variable in shape and number, were apparently covered by deciduous sheaths.

FORM. Pronghorn pelage is coarse. The medullary cell walls are denticulate; the cells themselves are large, hexagonal, and air-filled and thus provide excellent insulation (Murie, 1870). The hide is nearly worthless for leather. Pronghorns molt in the spring, the new hair is sleek and bright by late summer, but becomes pithy and dull by mid-winter. Females have two scent glands, one in each rump patch, which function with the rump patches in intraspecific communication; males have two rump glands plus two subauricular glands and one median gland, the latter three are important in sexual behavior (Moy, 1970 and 1971); both sexes possess interdigital glands on the forefeet and hind feet that produce sebum, which apparently conditions the hoofs (O'Gara and Moy, 1972). Pronghorns ordinarily have four mammae, but I have observed does with six. Cheekteeth are selenodont, hypsodont; dental formula is i 0/3, c 0/1, p 3/3, m 3/3, total 32 (Dow and Wright, 1962). Orbits are large; the lacrimal canal has one orifice inside the rim of the orbit; the lacrimal bone is separated from nasal by a vacuity; there is no sagittal crest; a postorbital bar is present; the basicranial axis is bent; lateral toes

are absent but lateral remnants of metacarpals are present; a cannon bone is present; front feet and hind feet are subequal in length; the ulna is reduced distally and fused to radius; fibula also reduced to distal nodule only; a gall bladder is present (O'Gara and Matson, 1975). The stomach is four-chambered and the uterus is bicornuate. Murie (1870) described in detail the skeletal, respiratory, and digestive systems as well as the urogenital system of the male. O'Gara (1968:13–20) described the female reproductive tract.

FUNCTION. Water consumption varies inversely with the quantity and succulence of preferred forage. In Utah, when forbs were abundant and their moisture content was 75% or more, pronghorns did not drink although water was readily available. During extremely dry periods, water consumption reached 3 liters per animal per day (Beale and Smith, 1970). Sundstrom (1968) found that pronghorns in the Red Desert of Wyoming consumed from 0.3 liters of water per day in May to 4.5 in August; most pronghorns remained within 5 to 6 km of water, but adult males were occasionally seen 10 km from any apparent source of water. Water flux is similar to that in domestic sheep and mule deer (*Odocoileus hemionus*), but noticeable differences exist between water kinetics of males and females; under test conditions, pronghorns had slightly higher content of body water than reported for other ruminants, possibly because of lower fat content than most domestic or laboratory animals (Wesley et al., 1970). Normal body temperatures of two does were established by telemetry as 38.5°C (Lonsdale et al., 1971). Fasting metabolic rates of four pronghorns ranging from 108 to 182 days of age were above the interspecies mean of 70 (kcal/kg/day times $W^{0.75}$, where W is total weight in kilograms), but similar results have occurred with other wild ruminants; heat production was comparatively high, possibly related to the high metabolism of young animals (Wesley et al., 1970). The concentration and percentage distribution of volatile fatty acids in pronghorn rumens correspond to those of domestic ruminants on somewhat comparable diets, but some statistically significant differences ($P < 0.05$) were obtained on the percentage distribution of the acids of adults and fawns (Nagy and Williams, 1969). The average vitamin A potency of fresh pronghorn liver during winter in Oregon was 1024 International Units per gram; during late spring and early summer, potency dropped 20%; in September, the average of 25 livers was more than 2200 I.U. per gram; the possibility of vitamin A deficiency appeared remote (Weswig, 1956). Trout (1976) analyzed blood from 22 pronghorns trapped in Idaho and Barrett and Chalmers (1976) analyzed blood from trapped adults (A) and neonates (N) in Alberta with the following results:

		n	mean ±	s.d.	unit/mm³
Total protein	—	22	64.5	5.5	μg
	A	20	65.3	11.2	μg
	N	46	47.8	5.6	μg
Glucose	—	22	2.16	.62	mg
	A	27	2.13	.838	mg
	N	26	1.57	.969	mg
Urea nitrogen	—	22	7.5	2.5	ng
	A	27	3.76	.577	ng
	N	27	1.62	.565	ng
Calcium	—	22	106.5	10.8	ng
	A	27	95.7	14.2	ng
	N	49	123.5	13.1	ng
Magnesium	A	27	16.0	4.80	ng
	N	49	22.2	2.80	ng
Sodium	A	27	3.54	.220	μg
	N	49	3.17	.322	μg
Potassium	A	27	216.0	78.6	ng
	N	49	239.0	356.0	ng
Phosphorus	A	26	53.8	18.3	ng
	N	49	91.1	20.7	ng
Cholesterol	A	27	577.8	132.3	ng
	N	56	693.0	413.0	ng
Red blood cells	A	130	11.55	1.26	×10⁶
	N	122	9.68	1.01	×10⁶
Leucocytes	A	130	5.17	1.88	×10³
	N	122	3.97	1.85	×10³
Albumen	A	20	40.6	4.7	μg
	N	46	23.6	3.4	μg
Hemoglobin	A	127	182.6	21.1	μg
	N	116	145.6	17.2	μg
Hematocrit	A	127	51.24	4.51	%
	N	110	39.70	3.94	%
Lymphocytes	A	125	31.65	11.91	%
	N	120	33.94	14.22	%
Neutrophils	A	125	64.39	12.72	%
	N	120	65.39	12.72	%

There were no significant differences in blood parameters between singles and twins at birth but considerable differences between sexes; leucocyte count, Na, K, and P had higher values in the blood of pronghorn neonates when the ambient temperature was < 10°C than when it was > 20°C, whereas blood urea nitrogen was higher at > 20°C than at < 10°C (Barrett and Chalmers, 1976).

ONTOGENY AND REPRODUCTION. Pronghorns are polygamous, females usually become sexually mature at approximately 16 months of age but occasionally conceive at approximately 5 months of age (Wright and Dow, 1962; Mitchell, 1967; O'Gara, 1968). The breeding period lasts from mid-September to early October in the north and late July to early October in the south (Lehman and Davis, 1942; Buechner, 1950). Gestation period in captivity averages 252 days (Hepworth and Blunt, 1966). Twins are more common than single births, ovulation and breeding are almost simultaneous, and does on good range usually ovulate four to seven ova; upon reaching the uterus, fertilized ova rapidly expand into blastocysts approximately 3 mm in diameter; at that stage, the thin walls of the blastocysts absorb nutrition from mucous in the lumen of the uterus; such mucous is plentiful during early pregnancy, allowing ova to develop for nearly a month before implantation. The walls of each blastocyst soon begin to elongate and form a tube about 125 mm long and 0.5 mm in diameter, the thread stage; at that time, the uterus is active and the fragile thread stage blastocysts are kneaded together and often tangle; such blastocysts sometimes form overhand knots or two threads form granny or square knots; the ends of threads with knots between them and the inner cell masses "bud-off" and become free vesicles; more than 20 such vesicles are sometimes found in one uterus. One fourth to one third of the ova generally die of malnutrition during the thread stage because their fetal membranes are so reduced by knotting and budding-off that they cannot absorb enough nutrition. Next, tubal walls thicken and diameters increase to nearly those of the uterine lumens; as the inner cell masses become embryos, they sink through the walls of the tubes, acquire amnions, and then float free within the chorions; cells on the outside of the chorions acquire brush borders to assist in absorption of food; embryos develop rapidly as new fetal membranes bud. The yolk sac, from the mid-gut, is a Y-shaped ribbonlike tube several times longer than the embryo before implantation; forks of the Y lie tightly against the chorion, apparently absorbing nutriments and transferring them to the gut. Each horn of the uterus has two expansions of the lumen, one near the *corpus uteri* (proximal chamber) and one near the oviduct (distal chamber); a rich supply of blood serves the uterine wall at the proximal chamber, fewer blood vessels supply the wall near the distal chamber (O'Gara, 1969a).

Quadruplets often survive the thread stage, and as many as seven embryos have been reported (Mitchell, 1965). If only two embryos survive, they both locate in the proximal chambers; implantation begins about a month after fertilization when embryos are approximately 5 mm long; fetal membranes of embryos in proximal chambers grow extremely fast; when a proximal embryo's necrotic tip reaches the membranes of a distal embryo, the tip usually pierces the distal chorion, folds in most of the length of the distal allantois, and carries the distal membranes and embryo to the oviduct where the embryo perishes from lack of nutrition. Pronghorns are the only animals known in which the number of embryos is normally reduced during pregnancy by the two methods described above (O'Gara, 1969a).

As implantation proceeds, chorionic villi in cotyledons give off short, leaflike secondary villi at right angles to the primary villi and the structure becomes dendritic, but the placenta remains epitheliochorial (Wislocki and Fawcett, 1949). Because maternal tissue is not destroyed during placentation, there is no bleeding at birth unless the birth canal is torn; the pronghorn placentome is of the flat or intermediate type; during pregnancy, the 90 or so caruncles (range 45 to 180) are arranged in four rows (O'Gara, 1969a). Fetal membranes of pronghorn twins join and fuse in the *corpus uteri* after they have passed the embryonic stage; during fusion of the membranes, the fetuses are approximately 50 mm long and 75 days old (O'Gara, 1968). After fetal membranes come together in the *corpus uteri*, the ends of chorions, in apposition to one another, degenerate and the amnions fuse; allantoes persist through mid-gestation as vesicles containing nitrogenous wastes from the fetuses; the corpora lutea grow to approximately 5 mm diameter during the first week after ovulation; if the doe becomes pregnant, slow but steady growth continues until birth of the fawns; at birth, corpora lutea measure more than 8 mm; one or two days later, they are reduced to spheres about 8 mm in diameter; six weeks later, the corpora albicantia appear as orange bodies less than 2 mm in diameter or as thin lines (O'Gara, 1968).

The amnion extrudes from the vulva for some time before the first fawn is born. The first part of a fawn to appear is usually the white-tipped front hoofs. Does lie down during most of the intense

labor, sometimes on their sides, and rock back and forth. Fawns are often born while does are recumbent, but does sometimes stand up after the foreparts of a fawn clear the vulva, and this allows the fawn to slide free; Kitchen (1974) observed five fawns that hung by their hips from standing does for two to six minutes before sliding free.

Fawns in Montana average about 3.5 kg at birth, but weights as light as 1 kg and as heavy as 5.8 have been recorded from other areas (Van Wormer, 1969). Such variations are probably related to range conditions, health of the doe and fetuses, and number of fetuses *in utero*.

Yearling males are capable of breeding (Wright and Dow, 1962), but fawns are generally considered incapable. However, testes of fawns are in the late prepubertal stage by November (O'Gara *et al.*, 1971). Yearling males seldom get a chance to breed because older bucks hold territories where most of the breeding takes place.

Testes of mature males vary in weight annually, averaging more than 40 g in July and August and less than 20 g in January and February; in Montana, spermatogenesis by yearlings and adults continues throughout the year but is limited in the period from December through February; by late March, tubules of the epididymides contain scattered to numerous spermatozoa; from April through November, epididymides are packed with spermatozoa; in December, they again become scattered and leucocytes appear, apparently "cleaning-up" degenerating spermatozoa; male pronghorns are apparently capable of ejaculating spermatozoa during much of the year; the short estrous period of females determines the breeding season (O'Gara *et al.*, 1971).

ECOLOGY. Some 35 million pronghorns inhabited North America before the arrival of white men, but by 1924, this population decreased to less than 20,000 animals. From 1924 to 1964, the population multiplied tenfold; recent increases occurred concurrently with annual harvests of twice as many pronghorns as existed in 1924. Numerically, pronghorns are the second most important big-game animal in North America. Effective law enforcement, habitat improvements, and wildlife management techniques aided population increases to approximately half a million pronghorns today (Yoakum, 1968). Yoakum (1972) plotted the 1964 estimated pronghorn populations on a map depicting the major vegetative communities of North America; 62% were on grasslands (41% short, 21% mixed); 37% on grassland-brushlands (33% bunchgrass-sagebrush, 1% grama-mesquite, 3% galleta-woodland); and 1% on deserts (hot and cold).

Pronghorns are dainty feeders, utilizing a wide variety of plants. Many studies of food habits have shown that northern pronghorns depend heavily on browse, particularly sagebrush, during winter. Bever (1951), Fichter and Nelson (1962), Wentland (1968), Bayless (1969), and Beale and Smith (1970) found that browse made up 80% or more of the winter diet. Hepworth (1970) found pronghorns utilizing winter wheat during winter where browse was not available. In Montana, Martinka (1967) observed pronghorn dying of malnutrition on grasslands and surviving on sagebrush ranges during a severe winter. Studies generally indicate that forbs are most important during summer; Beale and Smith (1970) found pronghorns utilizing forbs as 90% of their diet during summers of above-average rainfall in Utah, and only 20% during summers of below-average rainfall, browse making up the remainder. Baker (1953) found pronghorns using 86% browse during summer and autumn in Wyoming. Pronghorns use grass in early spring and occasionally in late summer if new growth appears. Hoover (1966) stated that ranges dominated by about equal proportions of browse plants and forbs, with some cacti and a minority of grasses, would provide the highest carrying capacities, considering only food habits. Southern pronghorns use more forbs and less browse than do northern pronghorns; considerable cactus is utilized in some areas (Terwilliger, 1953; Larsen, 1966). Hlavachick (1966) found Kansas pronghorns using 40% cactus, 22% grass (mostly wheat), 20% forbs, and 18% browse. Fichter and Nelson (1964), and Beale and Smith (1970), working in desert areas of Idaho and Utah, found positive correlations between fawn survival and precipitation during the previous year. Halloran and Glass (1959) found an inverse relationship between precipitation during May in Oklahoma and pronghorn survival. Pronghorns withdrew from Montana range used by sheep, but jointly used ranges with cattle (Campbell, 1970). Texas pronghorns fared well on overgrazed cattle ranches although their diet was altered; forbs increased on such ranges and pronghorns preferred that forage class; sheep eliminated many of the palatable forbs and sheep-proof fences restricted pronghorn movements. Pronghorn management and good range management go together; pronghorns are a valuable range asset because they utilize noxious weeds. Buechner (1947) reported that one cow utilized as much food as did 38 pronghorns. Long (1965) found that fire and mechanical disturbance increased production of forbs and thus increased use of those disturbed areas by pronghorns in South Da-

kota. Severson *et al.* (1968) found that domestic sheep and pronghorns were compatible in the Red Desert of Wyoming where the feeding habits of the two species were noticeably different. Pronghorns moved more than sheep and consumed 0.82 kg of oven-dried forage per day; 48.6 ha (120 acres) of desert could support eight pronghorns or 7.2 domestic sheep year-round under single use or six pronghorns and 6.2 sheep under dual use; one pronghorn consumed as much browse as did 5.67 sheep and one sheep used as much grass as did 43.5 pronghorns.

The timing and length of seasonal movements varies with altitude, latitude, and range conditions, but generally animals from large wintering herds disperse in spring. Deep snow sometimes forces pronghorns to move as much as 160 km from summering areas (Martinka, 1966). As snow melts, the animals move back to summer ranges. Natural barriers, such as steep timbered mountains and large bodies of water, impede pronghorn movements and such barriers determine, to some extent, the distribution. Fences, interstate highways, railways, and so forth further complicate movements and reduce the carrying capacity in areas where pronghorns must move long distances to procure the year-round necessities of life. Once on summer ranges, does generally collect into herds of a dozen or less; young bucks form slightly larger bachelor herds and old bucks claim territories.

Gregg (1955) found that Wyoming pronghorns remained on, or frequently ranged through, an area of 2.6 to 5.2 km² during summer and early autumn; their daily range, when undisturbed, was 0.2 to 0.6 km². Kitchen (1974) reported that territories in Montana ranged from 0.2 to 4.34 km². Those territories were located in relation to resources—small territories in areas with intervening ridges and large territories in flatter areas. Territories did not overlap and were widely spaced, generally with "no-man's" land between them. All territories that were used by does during the rut had open water. Bucks were most successful on territories where the terrain aided in cornering does; bucks were territorial from late March to October; territories provided the territorial bucks and any does with them sufficient forage. Territoriality has not been studied in southern populations. Marked and radio-tracked pronghorns studied by Bayless (1969) in Montana had winter ranges (km²) as follows: one yearling female, 22.5; one yearling male, 16.8; averages for six adult females, three female fawns, and five male fawns were 11.4, 9.8, and 6.5, respectively. Sizes of home and seasonal ranges vary so much with habitat and weather conditions that results from studies seldom have application to another area, or even another year.

Bachelor herds are usually composed of yearlings and two-year-olds, plus older males that have not acquired territories; bachelor herds have larger summer ranges than other pronghorn herds. Gilbert (1973) observed a bachelor herd with a stable hierarchy for seven weeks prior to the rut in Yellowstone Park; the herd was socially cohesive, but intensive and prolonged displays and sparring were common. The herd occupied poorer habitat adjacent to three territories held by large bucks, but commonly entered those territories during the rut to court estrous females. Bachelors are not tolerated on territories. Males attempt to acquire territories when three years of age in a Montana population studied by Kitchen (1974).

Formation of summering bands of does and fawns takes place gradually over a period of a few weeks. Lactating and nonlactating does herd together soon after fawns are born and utilize the summer ranges of several territorial bucks as well as areas around and between such territories. Thus, herds often appear to have one buck member. Mature females usually lead fleeing groups; if males are present, they bring up the rear. The usual shape of a fleeing herd is an ellipse, sometimes rather elongated (Gregg, 1955). Bromley (1967) concluded that fawns are functional members of the summer herds by the age of six weeks and have their own hierarchy. Many fawns are weaned during rutting activity, and small herds of fawns are common in autumn.

After the rut, territorial bucks leave their territories and all males cast their horn sheaths. Sizes of wintering herds are determined by geography, range conditions, and severity of winters. When snow gets deep, pronghorns usually must reach browse or perish. Thus, large herds gather on sagebrush ranges during some winters.

Behavioral adaptations enhance survival during severe northern winters. Pronghorns studied in Alberta were adept at pawing away snow to reach food; this occurred even when ample forage was available above the snow, probably allowing the animals to take advantage of the better quality of forage protected by snow cover. An established hierarchy at feeding craters reduced expenditure of energy. Pronghorn selected microhabitats with lower wind velocities, less snow, and softer and less dense snow than the average for the area. The animals conserved energy by reduced daily travel and single file travel in snow, and by lying down during postdawn periods of hard snow and low temperatures; clumped bedding patterns during high winds, lying with

head curled back alongside the body, and lying with heads oriented downwind reduced heat loss (Bruns, 1969).

BEHAVIOR. Territorial bucks (TBs) do most of the breeding, and establishment of territories is related to sexual behavior; however, bucks are territorial for a much longer period than is required to breed females. TBs defend their areas against intrusion by other males and mark tall vegetation on the territories with subauricular gland secretons. Elimination of urine and feces is accomplished during a linked sniff-paw-urinate-defecate sequence (SPUD); performed by TBs, the postural changes are extreme and each element of the sequence is exaggerated. Neither form of marking is used to indicate a specific boundary, but plants and scrapes are sometimes re-marked. The SPUD is often executed by bachelors as well as TBs. Bucks sometimes nose the spot where a doe has urinated, perform flehmen, and immediately SPUD on the urine soaked ground (Kitchen and Bromley, 1974).

A territorial buck's defense of its area is variable, but most encounters consist of part or all of five phases: 1) stare at intruder; 2) vocal display of TB's presence; 3) approach intruder; 4) interact with intruder; and 5) chase or withdrawal of intruder. Occasionally fights occur. All medium-sized animals, regardless of species, are watched closely as they enter a territory; TBs stare for as little as 10 seconds to more than 25 minutes before reacting to the presence of other animals. If the intruder is a pronghorn, the TB may utter a snort-wheeze (a loud, medium-pitched snort followed by a series of shorter bursts of sound descending in pitch and volume until termination). As they call, TBs pump their sides and probably their diaphragms. The snort-wheeze is usually associated with erection of the mane, the upper third of the rump patches, and hairs around the median gland. Intruding bucks sometimes abandon territories after just a snort-wheeze; yearlings flee more often than older bucks, and fewer bucks flee during the rut than earlier in the season. Dominant bachelor bucks sometimes use the snort-wheeze and TBs use it during courtship and while herding does (Kitchen and Bromley, 1974).

Encroaching males that do not leave a territory in response to a snort-wheeze are confronted by the TB, whose speed of approach depends on depth of intrusion into the territory and age of intruder; bucks well into a territory and yearlings elicit a rapid approach by the TB, which usually leads to running chases as intruders are driven from the area. Adult bucks near the edges of territories are approached more cautiously. TBs often lope or trot until within 40 to 80 m of an intruder. They then lower their heads, depress their ears and walk to within 15 to 25 m of intruding bucks; the walk then becomes a slow, stiff deliberate gait ending in a broadside threat similar to the threat display noted by Prenslow et al. (1968). If both bucks display, they are usually parallel or nearly so; parallel displays sometimes lead to parallel walking in a head-low posture and sometimes to a closer approach. By this time, intruding bucks have usually given ground. During some slow approaches, TBs thrash vegetation with their horns and mark vegetation with their cheek patches or perform the SPUD, or both; they often grind their teeth during a slow approach and occasionally stop to feed or give snort-wheeze calls. Territorial neighbors, and sometimes other intruders, mark, thrash, or feed as a TB approaches. When within 15 to 25 m of an intruder, TBs usually perform the same behavioral act as displayed by the other; many acts are then used and reused as the two bucks go through general patterns of feed-trash-mark-walk-threaten. Encounters are pushed as TBs move closer; in most interactions, the intruders no longer respond to the TB's initiative and simply watch. This usually leads to a strong threat and a herding of the intruder away at a walk or chasing him away at a run. Occasionally low guttural roars are uttered by TBs before or during a chase, especially preceding attempts to horn fleeing males. Chases range from a few meters to 5 km. When a TB is chased, dominance reversal occurs as its boundary is crossed (Kitchen and Bromley, 1974).

Occasionally, displays are not sufficient to scare an intruder from the territory and serious fights result. Kitchen and Bromley (1974) observed 15 fights, 14 occurred during the rut. Fights consisted of a series of thrusts and counterthrusts; the apparent goal was to gore the opponent. Prongs were not always large enough to catch an opponent's prong so some fights were horn-to-horn and some were head-to-head. Bucks tried to push their adversaries off balance by twisting their necks; each buck tried to gain an uphill advantage during battle. Fights only averaged two minutes, but five animals were seriously injured in the 15 fights. Kitchen and Bromley (1974) saw 11 other injured bucks, probably victims of fights; they also found carcasses of two large bachelor bucks with deep puncture wounds in their lungs and hearts.

As the rut approaches, a TB holds, or attempts to hold, does on his territory. A sexually aroused buck announces his intentions to the doe by emitting a high-pitched whine, which decreases to a low, guttural roar; simultaneously, the buck's body becomes rigid with legs straight, neck vertical, and nose horizontal; and the mane and hair of the median gland are erected. If the doe is receptive, she raises her tail and the buck approaches her rump with short prancing steps. At about 5 m, the buck starts waving his head laterally; head-waving is accompanied by a low sucking sound, a chewing motion, and tongue flicking. If the doe is in estrus, she stands with her hind legs spread slightly, occasionally looks at the approaching male, and then allows him to mount. Does immediately lose interest in bucks after being bred (Bromley and Kitchen, 1974).

Does not in estrus move away from courting bucks; a retreating doe usually lowers her head to near the vegetation twisting her neck at the same time; often she flicks her tail and slightly lowers her whole body. These acts are in sharp contrast to the raised head and stationary stance of a female in estrus. Bucks sometimes chase unreceptive does through a series of loops and curves, frequently hooking at them and uttering deep guttural roars; bucks occasionally knock does down during such chases (Bromley and Kitchen, 1974).

Even does in estrus run from groups of courting bucks, which are usually bachelors. Bachelors court does more rapidly and persistently than do TBs; chases by bachelors are often long and attract other bachelors. Such harassment undoubtedly contributes to the high breeding success of TBs; when bachelors chase does into territories, the TBs challenge the harassing buck(s), giving the does sanctuary (Bromley and Kitchen, 1974).

The pronghorn's territorial system is beneficial to the species in several ways. It insures that the largest and most aggressive bucks do most of the breeding (Bromley and Kitchen, 1974). This system provides a haven where does can escape the overzealous courtship of bachelor bucks during parturition, lactation, and the rut (Cole and Wilkins, 1958). Territories also keep bachelors from competing with pregnant or lactating does on the best range (Gilbert, 1973).

Several hours to a day before giving birth, a pronghorn doe chooses a birth site. Usually the herd moves on, leaving her alone, but sometimes pronghorns of all ages and both sexes remain in the area. A couple of hours before parturition, a doe walks with her tail upright and stands with her hind legs stretched backward more than usual. During this time, she moves nervously about the chosen birth site, lying down and getting up. Autenrieth and Fichter (1975) observed siblings born from 9 to 31 minutes apart. The doe usually begins to lick each fawn immediately after delivery. Neonates right themselves and orient on their mothers within a few minutes; fawns nurse for the first time from 24 to 107 minutes after birth. Both mother and young frequently get up and lie down, probably establishing mother-infant bonds by touch, smell, and sight. Does eat the afterbirth. At first, a doe licks the entire fawn, but licking of the anogenital region soon takes precedence over generalized licking and occurs at intervals for two to three weeks. During such grooming, fawns assume a distinctive rump-up posture and eliminate; the mother ingests the urine and feces directly, reducing odors of the fawn and thus the possibility of them being found in their beds by mammalian predators. Watched by their mothers, young pronghorns selected their own bedding sites from the first day. Does left their fawns for the first time three to six hours after parturition; at intervals varying from about one to six hours during the next 3 weeks or so, does return to the area where their young are bedded.

Except for the short periods with their dams, fawns generally remain alone until about six days of age, when they begin to form sibling bonds (Bromley, 1967). Fawns often rise and go to the doe when she is still several meters away, the distance increasing as the fawns get older. Six behavioral features characterize the mother-fawn reunion period: recognition, nursing, anogenital grooming, play, the relocation move, and the move to lie secluded (Autenrieth and Fichter, 1975). Young fawns at ease lie with their heads up and appear alert. When they see movement, they flatten out with their heads on the ground in the position often seen in photographs. Fawns in that position remain perfectly still with lowered ears and open eyes. Fawns can be touched or picked up after a careful approach until about the third day of life.

Fawns apparently recognize their mothers mostly by sight, although visual contact may be preceded by vocal communication and verified by smell during the nose-to-nose greeting. For does, identification of their offspring begins visually, but confirmation often, if not always, depends on sniffing of the rear end. The role of the doe in nursing is largely passive; she stands still with her back arched in a way that lowers her hindquarters and spreads her knees slightly. Nursing fawns exhibit the milk kick, but do not wag their tails or root the udder. The length of nursing bouts decreases significantly during the four months until fawns are weaned (Autenrieth and Fichter, 1975). Females frequently leave their fawns unattended, leading to the misconception that nearby does are "baby sitting." Kitchen (1974) observed that does associated with fawn groups only took an interest in their own young in an alert-alarm, flight situation; he frequently saw "baby sit-

ting" does leave fawn groups completely unattended for more than two hours.

Fawns develop balance and speed by playing during summer. Playing fawns perform exaggerated and excessive movements. The first play involves leaping and sudden changes in direction; running play includes elements of alarm and flight, such as stotting and flaring rump patches. Sparring and bunting begins when fawns are about three weeks old and the amount of play may reflect the condition of the animals or their environment; fawns play until early autumn but play is seldom seen on winter ranges (Autenrieth and Fichter, 1975). Bullock (1974) described locomotion in detail.

GENETICS. Karyotypes from skin biopsies of three animals shot in Montana and one from Texas gave similar results: $2N = 58$; autosomes include two subtelocentrics and 54 acrocentrics; the X chromosome is an acrocentric and the Y is a subtelocentric. One karyotype taken from a pronghorn at the Catskill Game Farm had a bimodal distribution with some cells possessing 56 chromosomes (Hsu and Benirschke, 1969). *A. americana* has a large acrocentric X chromosome as do the majority of known bovids, and the karyotype is similar to that found in several other bovids (Todd, 1975).

REMARKS. Because of its annually deciduous horn sheaths, the pronghorn is commonly classified in a separate family Antilocapridae; however, some members of all five subfamilies of Bovidae also shed outer portions of their horns, and development and structure of horns are essentially similar in pronghorns and other bovids (O'Gara and Matson, 1975). Biochemical research also has indicated that pronghorns are closely related to other bovids (Curtain and Fudenberg, 1973).

A vast majority of the present-day pronghorns belong to the subspecies *A. a. americana*. Goldman (1945) noted that "three somewhat isolated, finger-like southern extensions carry the general range of the pronghorn antelope as a species into Mexico. These peripheral extensions represent geographic races differing from the typical form and from one another only in comparatively slight details of size, color, and structure." The same can be said for the western race, *A. a. oregona*. Bailey (1932), in naming that subspecies, stated that "the animals show only slight and gradual variation over their entire range, and no sharp lines of difference between described forms can be found." Whether all five subspecies are valid is a moot question further complicated by indiscriminant transplants of *A. a. americana* into the ranges of other subspecies.

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