

Habitat requirements of desert bighorn sheep / by Craig W. McCarty and James A. Bailey

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HABITAT REQUIREMENTS OF DESERT BIGHORN SHEEP

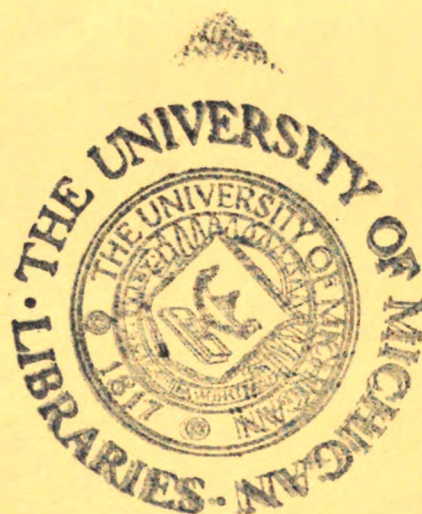
Craig W. McCarty
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May 1994



COLORADO DIVISION OF WILDLIFE
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HABITAT REQUIREMENTS OF DESERT BIGHORN SHEEP

by

Craig W. McCarty and James A. Bailey



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FOREWORD

In 1979, the Colorado Division of Wildlife, in cooperation with the Bureau of Land Management, began releasing desert bighorn sheep into southwestern Colorado. Depending upon whose history you believe, these releases were either reintroductions or introductions. There is some debate whether the original ranges of desert bighorn subspecies extended into Colorado. There is some archaeological evidence of desert bighorns in the southwestern part of the state, but to date no remnant desert bighorn populations have been identified in Colorado. It's possible indigenous desert bighorn herds were extirpated along with indigenous Rocky Mountain bighorn populations in the late 1800s. If desert bighorns did range into Colorado at one time, it was probably the northeastern limit to their range. Regardless of historic distributions, since their release at several Colorado sites beginning in 1979, desert bighorns have thrived.

The combination of habitat-related factors that caused desert bighorns to yield range to Rocky Mountain bighorns remains as uncertain as the boundary between the historic ranges of these two subspecies. Colorado offers a wide variety of habitats suitable for supporting bighorn sheep, as evidenced by the relative abundance of bighorns statewide prior to pioneer settlement. Yet desert bighorns were probably never as abundant here as their Rocky Mountain conspecifics. The short-term success of recent translocations suggest desert bighorn herds in southwestern Colorado can grow and expand; however, the long-term viability of these populations depends on the availability and condition of suitable habitat. What desert bighorn sheep regard as suitable habitat may differ markedly from what desert bighorn sheep managers regard as suitable habitat.

It follows that a comprehensive understanding of habitat requirements is critical to developing and choosing among strategies for effectively managing desert bighorn sheep in Colorado. Because historic information on desert bighorns in Colorado is quite limited and equivocal, we've needed to rely on observations from elsewhere in helping to shape this understanding. In this report, Craig McCarty and Jim Bailey have synthesized the available data, observations, and theories concerning important habitat requirements of desert bighorn sheep. They have identified incongruities between data and beliefs about desert bighorns and their habitats, as well as gaps in our knowledge about those relationships. This review formed the basis for development of a quantitative approach for evaluating and comparing prospective sites for desert bighorn reintroduction. Such an approach should aid the Division of Wildlife, the USDI Bureau of Land Management, and other management agencies in restoring and maintaining desert bighorn sheep throughout historic ranges in Colorado and elsewhere.



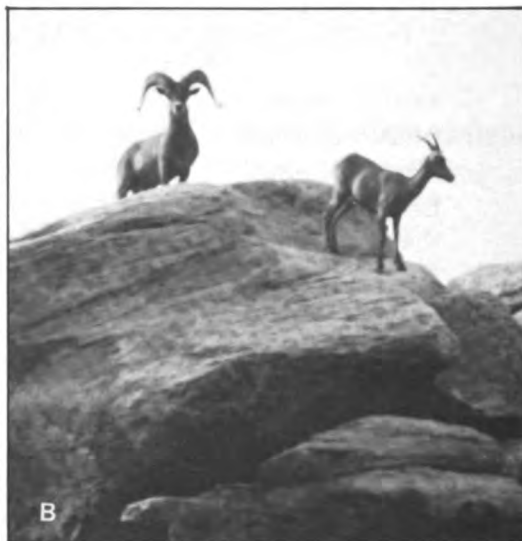
Bruce Gill
Wildlife Research Leader

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Frontispiece. Desert bighorn: (A) 2 ewes and 5 lambs, Dolores River Canyon, Colorado (transplant from Lake Mead, Nevada, 1986); (B) ram and ewe, Dolores River Canyon, Colorado; (C) states where desert bighorn are found; (D) 14 rams, Red Rocks, New Mexico; (E) ram at water guzzler, New Mexico. Photos A and B by Craig McCarty, D by Amy Fisher, and E by William Dunn.

HABITAT REQUIREMENTS OF DESERT BIGHORN SHEEP

This review of literature on the habitat requirements of desert bighorn sheep (*Ovis canadensis* spp.) emphasizes citations since 1980. Previous literature has been reviewed in Monson and Sumner (1980).

For organization, the habitat of desert bighorn is described as distinct HABITAT COMPONENTS (topographic cover, forage, water sources, thermal cover, and mineral sources) and HABITAT CHARACTERISTICS (i.e., visibility, seral stage, and interspecies conflicts). Habitat characteristics are further classified as (1) unique characteristics, which apply to only 1 habitat component, and (2) general characteristics, which apply to 2 or more habitat components. We review unique habitat characteristics with each habitat component.

General habitat characteristics are discussed separately.

For most habitat components and characteristics, information on the "artificial" subspecies (Ramey 1991, 1993), or ecotypes, of desert bighorn is combined. Forage species used by desert bighorn are an exception. The terms "mountain bighorn" and "desert bighorn" refer to Rocky Mountain bighorn sheep (*O. c. canadensis*) and desert bighorn sheep (*O. c. nelsoni*, according to Ramey 1993), respectively, while the term "bighorn" refers to both.

There are at least 13 habitat suitability models for desert bighorn (Table 1). These models are referenced frequently in this text as "models of desert bighorn habitat" without repeating their citations.

HABITAT COMPONENTS

TOPOGRAPHIC COVER

Topography is the primary source of bighorn cover for bedding, lambing, and escape (Geist 1971, McQuivey 1978, Hansen 1980a, Wilson et al. 1980, Van Dyke et al. 1983). However, definitions and interpretations of topographic cover vary among models of desert bighorn habitat (Table 2). Most definitions are in terms of (1) presence of escape terrain, (2) average slope, (3) physiographic type and ruggedness, or (4) aspect.

Definitions of Escape Terrain

No definition of escape terrain is widely accepted. Most definitions emphasize steepness and brokenness of terrain. Criteria of slope steepness have been highly variable, ranging from 50 to >300% (Table 3). In addition, total area, has been suggested as important for escape terrain. No author, or habitat model, considers all 3 of these characteristics (Table 3).

Dimensions of Escape Terrain. – Two authors used a minimum area in definitions of escape terrain (Tilton 1977, 1.6 ha; Armentrout and Brigham 1988, 2 ha; Table 3). Average dimensions of escape terrain used by mountain bighorn in Colorado (McCollough 1982; Table 3) provide an area of 1.26 ha.

Dunn (1991) considered escape terrain to be the best habitat component for estimating potential pop-

ulation size. He observed, in 2 New Mexico populations, 5.8 and 7.9 bighorn/km² of escape terrain (W. Dunn, pers. commun.). Holl (1982) and Wakelyn (1984) found correlations between population sizes and amounts of escape terrain within bighorn home ranges. Holl's equation is: Ewes ≥ 1 year old = escape terrain (ha) on winter range $\times (0.179) - 1.43$. It predicts that 50 desert bighorn ewes will use 287 ha of escape terrain on winter range. In contrast, Dunn's observation (above) predicts that 50 desert bighorn, of both sexes, use 633-862 ha of escape terrain on year-round range.

Preference for Steep Slopes

Four frequently reported observations suggest the importance of steep slopes to bighorn: (1) descriptions of bighorn behavior in selecting bedsites or lambing areas, and in response to perceived danger, (2) a high frequency of observations proximate to escape terrain (Table 4), (3) a high frequency of observations on steep terrain (Table 5), and (4) correlations of bighorn heart rates with distance from escape terrain.

It is unclear if topographic cover for bedding, or for lambing, is significantly different from terrain used only for escape. Bighorn most frequently select steep terrain for lambing sites (Geist 1971, Ravey 1984, Etchberger 1993). Wilson et al. (1980) and Armentrout and Brigham (1988) suggested that

Table 1. Habitat suitability models for desert bighorn.

Model	Comments
Ferrier and Bradley (1970).	Developed from, and used to evaluate occupied desert bighorn habitat in Highland Mountain Range, Nevada.
Breyen (1971). Cited by Hansen (1980b), original not seen.	Used to evaluate potential desert bighorn habitat in Eldorado Mountains, Nevada.
Grunigen (1980), modification of Hansen (1971) ¹ .	Used to evaluate potential bighorn habitat in northern Nevada.
Hansen (1980b).	Developed from, and used to evaluate occupied desert bighorn habitat in Desert National Wildlife Refuge, Nevada.
Golden and Tsukamoto (1980), modification of Hansen (1980b).	Used to evaluate potential desert bighorn habitat in Sante Fe National Forest ranges, northern New Mexico. Used by Gray (1988) and Stevenson (1988) to evaluate potential habitat in south-central Nevada.
Holl (1982).	A PATREC ² model developed from, and used to evaluate occupied desert bighorn habitat in the San Gabriel Mountains, California.
Brown (1983).	Used to rate potential transplant sites in Arizona.
Cunningham (1989), modification of Brown (1983).	Used to evaluate occupied desert bighorn habitat in 8 Arizona mountain ranges.
Cunningham (1989), modification of Hansen (1980b).	Predicted use of habitat by desert bighorn in Superstition and Eagletail Mountains, Arizona.
Armentrout and Brigham (1988).	Developed to evaluate habitat in the Basin and Range Province, Nevada.
Wakeling and Miller (1990), modification of Cunningham (1989).	Based on desert bighorn use/availability data from the Superstition Mountains, Arizona.
Dunn (1991).	Based on literature review; used to evaluate 10 potential and 1 occupied ranges in New Mexico.
McCarty (1993).	Based on literature review and results of field evaluation of Armentrout and Brigham (1988). Predicted habitat use by desert bighorn ewes in Dolores River Canyon, Colorado.

¹ Same as Hansen (1980b)

² PATREC = pattern recognition (Kling 1980).

lambling areas are steeper than areas considered only as escape terrain. Creeden (1986) made no distinction between lambing topographic cover and escape terrain, only stating: "Ewes preferred inner-canyon habitats for lambing. They most often selected ledges at the bases of sheer canyon walls and above steep talus slopes. All sites were located on escape terrain."

Bedding areas are frequently on steep terrain (Merritt 1974, Wakeling and Miller 1989). Wakeling and Miller (1989) reported that the upper 2/3 of terrain features were favored (relative to availability) for bedsites. Etchberger (1993) found among-years fidelity of ewes to specific lambing areas.

Use of escape terrain varies with group size (Risenhoover and Bailey 1985), group composition,

and season (Hansen 1982, Cunningham and Ohmart 1986). It is not clear if this variation is consistent across herds. Sandoval (1980) observed bachelor ram groups venturing further from escape terrain than did ewe-lamb groups. In contrast, Tilton and Willard (1982) observed wintering adult ram groups nearer to "cliffs" (interpreted as escape terrain) than were wintering young ram and ewe-juvenile groups. Wakelyn (1984) tabulated reported distributions of bighorn in relation to distance from escape terrain, and concluded: "The importance of slope steepness evidently depends on a variety of factors, including availability, season, time of day, sex/age groups and activities in which bighorn are engaged." This conclusion is supported by more recent information (Tables 4, 5).

Tilton and Willard (1982), related use of slopes by mountain bighorn to slope availabilities. They demonstrated a preference for slopes >80%, a preference for areas <320 m from escape terrain, and an avoidance of areas >320 m from escape terrain. Similarly, McCarty (1993) demonstrated a preference of desert bighorn for slopes >84% and areas <5 m from escape terrain, and an avoidance of slopes <36% and areas >105 m from escape terrain. Also, Wakeling and Miller (1990) demonstrated a preference of desert bighorn for slopes >70% and avoidance of slopes <30%.

MacArthur et al. (1979, 1982) and Stemp (1983) correlated heart rate of mountain bighorn positively with distance from escape terrain. Consequently, the strong association of bighorn with escape terrain and precipitous slopes may be a psychological response to the threat of predation. No literature suggests to what degree this response might be modified as bighorn learn to use areas where predation or other harassment is absent.

Aspect

In northern areas, and where trees and tall shrubs may become dense, bighorn generally prefer south aspects (McCollough et al. 1980, Holl 1982, Wakelyn 1984). Wakelyn (1984) reviewed reports of aspect selection by bighorn and concluded: "When availability has been considered, bighorn preference for southern aspects has been consistent." and "Use of various aspects by bighorn sheep appears to be fairly consistent among areas, seasons, elevations, time of day, and sex/age groups." South-facing slopes are generally warmer, have less snow in spring and winter, and support open vegetation types providing good visibility. Lack of snow and good visibility enhance forage acquisition by bighorn (Risenhoover and Bailey 1985, Goodson et al. 1991).

Tilton and Willard (1982) reported that south aspects were strongly preferred, relative to availability, while east and southeast aspects were avoided, by a wintering mountain bighorn herd in Custer State Park, South Dakota. Hansen (1982) reported a seasonal change in the aspects of slopes selected by bighorn in the Sheldon National Wildlife Refuge, Nevada.

Table 2. Characterizing features of topographic cover, for desert bighorn according to 13 habitat models.

Habitat model	Variable(s) used to characterize topographic cover
Ferrier and Bradley (1970).	Average slope.
Breyen (1971).	Ruggedness and average slope.
Grunigen (1980).	Physiographic type.
Hansen (1980b).	Physiographic type.
Golden and Tsukamoto (1980).	Physiographic type.
Holl (1982).	Total area of escape terrain.
Brown (1983).	Presence of escape terrain, lambing grounds, and elevational relief.
Armentrout and Brigham (1988).	Physiographic type, and presence of escape terrain.
Cunningham (1989), modification of Brown (1983).	Presence of escape terrain, lambing grounds, and elevational relief.
Cunningham (1989), modification of Hansen (1980b).	Physiographic type.
Wakeling and Miller (1990).	Physiographic type, average slope, and presence of escape terrain.
Dunn (1991).	Presence of contiguous escape terrain and ruggedness as indicated by aspect diversity.
McCarty (1993).	Presence of escape terrain.

In hot deserts, aspect has not consistently influenced bighorn distribution. Wakeling and Miller (1990) found no significant relationship between habitat use and aspect in the Superstition Mountains of Arizona. In southwestern New Mexico, Watts (1979b) found bighorn preferring aspects from east to southeast; whereas Elenowitz (1984) reported that north, south, west, and northwest aspects were preferred, relative to availabilities. However, Elenowitz (1984) also reported that no preference was demonstrated for any aspect within individually delineated home ranges ("exploratory sallies, travel routes, and flat country excursions" were not considered in calculating these home ranges). Only 1 model of desert bighorn habitat (Holl 1982) considers aspect.

Physiographic Type and Ruggedness

Hansen (1982) found bighorn, especially ewe-lamb groups, preferred (relative to availabilities) physiographic types characterized by presence of

escape terrain on the Sheldon National Wildlife Refuge, Nevada. Similarly, Wakeling and Miller (1990) found desert bighorn preferred landforms classified as ridge tops, canyon slopes, and mountain slopes in the Superstition Mountains, Arizona. Three methods for characterizing ruggedness of bighorn topographic cover are (1) word models describing land forms (Hansen 1980b, Armentrout and Brigham 1988); (2) variation of micro-aspect (Dunn 1991); and (3) density of topographic contour lines on maps (Beasom et al. 1983, Warrick and Krausman 1987, Haas 1991).

WATER

Most authors, and all models of desert bighorn habitat, consider free water (streams, permanent pools, guzzlers, etc.) as a necessary component of desert bighorn habitat. Desert bighorn numbers and distributions have responded to an increase in the availability of water in the River Mountains, Nevada (Leslie and Douglas 1979); and to a decline in water availability in Death Valley (Douglas 1988). Bighorn distributions have been correlated with proximity to water sources (Table 6). Wakeling and Miller (1990) found desert bighorn preferred habitat closer to water, in the Superstition Mountains, Arizona. In contrast, Krausman and Leopold (1986) found water more abundant on areas available to, but not used by, bighorn in the Harquahala Mountains, and Etchberger found bighorn made little use of water developments in the Little Harquahala Mountains where permanent free water is unavailable. They suggested that free water was not a limiting factor in these Arizona ranges.

Water Source Characteristics

The definition of an acceptable water source for desert bighorn is not clear. Armentrout and Brigham (1988) suggest an ideal water source be "sufficient and always present." While the need for "sufficient" water is frequently recognized, only 1 source quantifies this term. Dunn (1991) suggested that a sufficient water source must maintain "the equivalent of a pool of surface water ≥ 1 m in diameter and ≥ 8 cm deep during the hot dry season." Turner (1973) concluded that desert bighorn must replace at least 4% of body weight daily to maintain water balance during summer. Therefore, if water is replaced by drinking, and given an average body weight of 61 kg (Hansen 1980c), a "sufficient" water source must provide at least 2.4 l/desert bighorn/day. Ferrier and Bradley (1970) consider water quality as an important characteristic of water sources for desert bighorn. In most models of desert bighorn habitat, water sources are rated according to seasonal perma-

Table 3. Definitions of desert bighorn escape terrain used in research.

Definition	Comments and reference
Terrain steeper than 80%, at least 1.6 ha in size.	Tilton (1977).
Terrain steeper than 100% with cliffs and rockslides.	Harrington (1978).
Steep, rocky, broken terrain with dry drainageways.	Hansen (1980b).
Slopes with rocky outcrops or cliffs.	Haas (1980).
Steep cliffs at least 8 m high and 200 m long, characterized by sparse vegetation.	Defined according to bighorn use. McCollough et al. (1980).
Any cliff or rock outcrop >3 m high and >30 m long.	Hansen (1982).
Slopes $>60\%$ and dominated by rock outcrops.	Holl (1982).
Steep cliffs or rock outcrops: average dimensions of 16 m high, 790 m long, and 72° (308%) slope.	Defined according to bighorn use. McCollough (1982).
Slopes $>80\%$.	Brown (1983).
Rough, broken topography, including caves, rock outcrops, and ravines.	Elenowitz (1984).
Rocky and broken ground with slope $>200\%$.	Risenhoover and Bailey (1985).
Steep ($>55\%$), rocky, broken terrain.	Gionfriddo and Krausman (1986).
Steep ($>60\%$), broken escarpments or outcrops ≥ 2 ha, with traversable terraces.	Armentrout and Brigham (1988).
Rough, rocky terrain with slope $>50\%$.	Wakeling and Miller (1990).
Areas with $\geq 60\%$ slopes.	Dunn (1991).
Any change in elevation ≥ 60 m (200 ft) with slope of $\geq 60\%$.	McCarty (1993).

Table 4. Distribution of desert bighorn in relation to distance from escape terrain.

Distance from escape terrain (m)	Observations (%)	Location and (Reference)
< 5	56	Dolores River Canyon, Colorado (McCarty 1993).
< 55	66	
< 105	79	
< 25	82	Superstition Mountains, Arizona (Wakeling and Miller 1989, 1990).
< 25	81	
< 50	61	Arches National Park, Utah (Haas et al. 1990). Escape terrain defined according to Gionfriddo and Krausman (1986).
< 75	91	Peloncillo Mountains, New Mexico, (Elenowitz 1984).
< 100	76	San Andres Mountains, New Mexico, (Sandoval 1980).
< 100	64	
< 200	98	
< 100	91 (74,99) ¹	Sheldon National Wildlife Refuge Nevada (Hansen 1982).
< 100	67 (35,84) ¹	
< 100	57 (31,79) ¹	
< 100	39 (29,93) ¹	
< 600	99.9	Canyonlands National Park, Utah (Bates and Workman 1983).
< 1300	100	River Mountains, Nevada (Leslie and Douglas 1979).

¹(Percent of observations when vegetation height was <20cm - affording good visibility, percent when vegetation was >30cm - affording poor visibility.)

nence, without further definition. Holl (1982) is an exception; in this model water must only be "available."

Variation in Water Use

Use of free water and proximity of desert bighorn to free water varies seasonally and between sexes (Table 6), and reported watering rates vary across herds (Turner and Weaver 1980). Water is available to bighorn metabolism from (1) free (standing or running), (2) early morning condensation, (3) a by-product of oxidative metabolism, and (4) in forage (Turner and Weaver 1980). The capabilities and mechanisms of water acquisition by desert bighorn are not clear. Krausman et al. (1985), Etchberger (1993), and Watts (1979a) documented herds of desert bighorn living without access to permanent free water. In these reports, use of succulent plants was suggested as an alternative to free water. Observations of Warrick and Krausman (1989) support this suggestion. Investigating 1 of

these herds, Alderman et al. (1989) found no relationship between ewe activity patterns and forage moisture content. However, forage moisture was consistently high throughout the day. They concluded that these desert bighorn ewes may obtain about the same amount of water from their forage at any hour of the day.

FORAGE

Characteristics of Foraging Areas

It is difficult to define an ideal forage resource for desert bighorn. An ungulate foraging area may be defined by size and (1) forage density and quality, (2) species composition and diversity, and (3) the spatial arrangement of forages. No model of desert bighorn habitat uses all these characteristics. In most models, foraging habitats are rated according to the abundance of grasses, or grasses and forbs. This abundance may be measured directly, or indirectly according to a scale of vegetation types in which

Table 5. Distribution of desert bighorn in relation to steepness of slope.

Slope (%)	Observations (%)	Location and (Reference)
> 100	42	Carrizo Canyon, California (Cunningham and Ohmart 1986).
> 100	91	Winter
> 100	71	Spring
		Summer
> 73	69	Colorado National Monument, Colorado (Ravey 1984).
> 69	44	Superstition Mountains, Arizona (Wakeling and Miller 1989), bedsites.
> 30	88	
> 69	27	Superstition Mountains, Arizona (Wakeling and Miller 1990).
> 30	82	
21-50	63	Peloncillo Mountains, New Mexico (Elenowitz 1984).
20-60	65	San Andres Mountains, New Mexico (Sandoval 1980).
> 20	64-85	Range for 4 areas in Big Hatchet Mountains, New Mexico (Watts 1979b).

types having abundant grasses and forbs are rated higher.

Forage density and quality. – The size of a foraging area and its density of forages may determine its carrying capacity for bighorn. Steel and Workman (1990) concluded that forage quantity did not influence microhabitat use by desert bighorn in Capital Reef National Park, Utah. However, this herd was not at carrying capacity and forage may not have been a limiting factor.

Hobbs and Swift (1985) proposed an algorithm for estimating carrying capacities for mountain bighorn from forage density and quality. They concluded: "reliable evaluation of relationships between range food supplies and animal food requirements must treat forage amount and quality as integrated rather than distinct features of habitat."

Species composition and diversity. – Desert bighorn are opportunistic and adaptable feeders (Krausman et al. 1989, Leslie and Douglas 1979, Cunningham 1989, Miller and Gaud 1989). Brown-ing and Monson (1980) reviewed diet studies and concluded: "Generalities about the food habits of desert bighorn over their entire range are difficult to make because of the tremendous variety in both composition and density of the flora in the expanse of the range they inhabit." The proportions of grasses, forbs, browse, and succulents consumed vary among areas occupied by desert bighorn, and also among seasons (Table 7, Miller and Gaud 1989). Grasses appear more important in diets of bighorn in Nevada, and when seasonally abundant elsewhere. Browse has dominated the annual diets reported

from 9 study areas in Arizona, New Mexico, south-eastern Utah, and southern California (Table 7). Selection of forage species by males and females is similar in some, but not all, areas (Smith and Krausman 1987, Krausman et al. 1989, Miller and Gaud 1989, Etchberger 1993). Rams, because they are larger, require more energy and nutrients compared to ewes and juveniles (Hanley 1982). This may cause rams to forage in different habitats and to select different, more abundant, forage species; or to forage more continuously.

In recent studies, 8 grass species, 11 forb species, 18 browse species, and 3 succulent species have been noted as principal forages of desert bighorn (Tables 8-11).

In at least 4 studies, forage availabilities were measured to estimate forage preferences of bighorn. Bates and Workman (1983) reported that desert bighorn in Canyonlands National Park, Utah, used forbs significantly more, and shrubs significantly less, than expected based on availabilities. In contrast, Rominger et al. (1988) reported that a herd of mountain bighorn at low elevation in Colorado used browse, during summer, more than expected based on availability. Elenowitz (1983) reported that shrubs were preferred over grasses and that forbs were used in proportion to their availability by desert bighorn in the Peloncillo Mountains, New Mexico. In Arizona, Miller and Gaud (1989) found 7 plant taxa that were consistently preferred in comparisons among years, areas, and between sexes. However, they reported that some frequently used forage species were not rated as "preferred" because they were very abundant. Miller and Gaud (1989) suggested

Table 6. Distribution of desert bighorn in relation to distance from water.

Distance from water (m)	Observations (%)	Location and (Reference)
< 400	47	Superstition Mountains, Arizona (Wakeling and Miller 1989), bedsites.
< 800	79	
< 400	44	Superstition Mountains, Arizona (Wakeling and Miller 1990), all observations.
< 800	84	
< 800	94	Canyonlands National Park, Utah (Bates and Workman 1983).
< 800	70	Sheldon National Wildlife Refuge, Nevada (Hansen 1982).
< 1000	90	
< 1500	83	Carrizo Canyon, California (Cunningham and Ohmart 1986). Summer
< 2500	60	Winter
		San Andres National Wildlife Refuge, New Mexico (Sandoval 1980). May-October
< 1500	88	Ewe-lamb groups
< 1500	88	Breeding groups
< 1500	94	Adult ram groups
		November-April
< 1500	93	Ewe-lamb groups
< 1500	93	Breeding groups
< 1500	79	Adult ram groups
< 1600	96	Peloncillo Mountains, New Mexico (Elenowitz 1984).
< 1600	49	River Mountains, Nevada (Leslie and Douglas 1979), Jun-Aug.
< 3200	84	

that desert bighorn are such adaptable foragers that the species composition of a range may not be important so long as a sufficient biomass of "fairly diverse vegetation" is present. This conclusion assumes that there is little difference in forage quality among most potential forage species, or that a "fairly diverse vegetation" always contains sufficient high-quality forages.

Spatial arrangement of forages. – Risenhoover and Bailey (1985) suggested that forage for mountain bighorn should be "abundant and continuously-distributed" to support "desirable large group sizes," but did not quantify these terms. They suggested forage continuity (as opposed to patchiness) allows a desirable spacing among individuals, and that spacing enhances predator detection and reduces the frequency of social behavior that interferes with foraging. The observations of Warrick and Krausman (1987) support this hypothesis.

Forage Quality Requirements

In a pen, an adult desert bighorn can consume

1.3-1.8 kg of dry alfalfa, or 1.1 kg of dry grass, daily (Hansen 1980a, Krausman et al. 1988). Hebert (1973) reported dry mater intake of 1.9 kg/day and nitrogen intake of 17 g/day for mountain bighorn. However, Mazaika et al. (1992) reported higher daily consumption rates of native forages for 2 captive adult male desert bighorn: Spring, 3.87 kg/day; Summer, 2.66 kg/day; Fall, 2.91 kg/day; and Winter, 4.21 kg/day. Hobbs and Swift (1985) suggested an average metabolic rate for bighorn of 22,094 kJ/day (838 kJ/kgBW^{0.75}/day), or twice the standing metabolic rate reported by Chappel and Hudson (1979). Krausman et al. (1988) observed daily intake by 3 desert bighorn rams of 10,411-16,056 kJ (627-643 kJ/kgBW^{0.75}).

Krausman et al. (1989) determined seasonal levels of protein, fiber, ether extract, and ash in 29 forage species used by desert bighorn. A nutritional index based on these forage components explained little of the variation in food habits.

No models of desert bighorn habitat rate foraging areas according to their nutritional/caloric dimensions.

Table 7. Relative frequencies of forage classes in diets of desert bighorn.

Grasses (%)	Forbs (%)	Browse (%)	Succulents (%)	State	Location and (Reference)
16	27	51	6	Arizona	Aravaipa Canyon (Dodd and Brady 1988);
13	24	60	3		Annual,
17	34	44	5		Spring,
17	23	50	10		Summer,
					Autumn.
				Arizona	Bill Williams Mountains (Seegmiller and Ohmart 1982);
2	59	38			Spring,
6	53	37			Lambs,
					Adults, yearlings,
10	17	72			2 Summers,
16	16	56			Lambs,
					Adults, yearlings.
38	3	56		Arizona	Death Valley National Monument (Ginnett and Douglas 1982),
					Annual diet.
				Arizona	Little Harquahala Mountains, annual diet, ewes;
2	36	62 ¹			(Krausman et al. 1989)
3	36	58 ¹			Annual ewes,
					Annual rams,
11	36	54 ¹			(Etchberger 1993)
11	33	56 ¹			Annual ewes,
13	23	64			Annual rams.
17	54	27	2	Arizona	Sonoran Desert (Miller and Gaud 1989), annu. diet, rams and ewes.
				Arizona	Virgin Mountains (Smith and Krausman 1987).
2	32	57	8	California	Carizo Canyon (Cunningham and Ohmart 1986).
				California	San Gabriel Mountains (Perry et al. 1987);
22	2	60			Annual,
26	0	64			Spring,
28	1	58			Summer,
28	0	54			Autumn,
10	0	75			Winter.
73	5	23		Nevada	Pinwater Mountain Range (McQuivey 1978).
42	40	14		Nevada	Sheldon National Wildlife Refuge (Hansen 1982).
57	33	10		Nevada	Southern (Brown et al. 1977).
				N. Mexico	Big Hatchet Mountains (Watts 1979b);
19	35	46			Annual diet,
55	37	8			July,
25	74	2			September,
5	10	86			March.
21	11	68		N. Mexico	Peloncillo Mountains (Elenowitz 1983), annual diet.
				N. Mexico	San Andres National Wildlife Refuge (Sandoval 1980);
10	30	56			Spring,
16	29	50			Summer,
9	48	38			Fall,
7	33	55			Winter.
38	19	43		Utah	Canyonlands National Park (Bates and Workman 1983).
				Utah	Southeastern (King and Workman 1982);
11	35	53			Annual,
18	6	76			Summer,
28	2	70			Autumn.

¹Succulents included in this figure.

Foraging Efficiency

Foraging efficiency of bighorn is defined as the rate of intake of energy and of nutrients per unit of time, or per unit of energy expended (Dale and Bailey 1992). Four measures of foraging efficiency are:

1. Energy-intake efficiency (kcal/min or kcal/step),
2. Nutrient-intake efficiency (g/min or g/step),
3. Energy intake per day,
4. Nutrient intake per day.

Foraging efficiency is determined by 7 interrelated components:

1. Time efficiency: the percent of a foraging bout devoted to foraging effort – as opposed to alert or social behavior. This component is influenced by habitat security and by group size (Risenhoover and Bailey 1985),
2. Cropping rate (bites/min),
3. Biomass-intake rate (g/min), influenced by cropping rate and bite sizes,
4. Search effort (steps/bite),
5. Foraging effort (steps/g of intake),
6. Time effort (hours of foraging bouts/day),
7. Forage quality (digestible energy and nutrients/g).

Dale and Bailey (1982) referred to the characteristic of a forage that allows a high biomass-intake rate as "forage harvestability." Harvestability is determined by the sizes of potential bites of forage, and their density in 3-dimensional space. From the point of view of foraging efficiency, an optimum bighorn forage (1) occurs in a secure habitat; (2) is abundant in the habitat so as to support a large group of bighorn; (3) is palatable; (4) has a high density of digestible nutrients and energy; (5) provides large bite sizes; and (6) is densely-distributed at each foraging site. The large variation of forages consumed and preferred by bighorn probably reflects, not only "variation in both composition and density of flora" in desert bighorn ranges (Browning and Monson 1980), but also variation and "tradeoffs" in the above 6 components of forage quality.

Forage selection by bighorn appears to be a complex process. If bighorn forage to maximize some aspect of foraging efficiency, they may select habitats and foraging group sizes, and alter search effort, time

Table 8. Principle or representative grasses consumed by desert bighorn.

Grass	Location and (Reference)
Cottontop <i>Tricachne californica</i>	Chihuahuan Desert (Browning and Monson 1980).
Galleta <i>Hilaria rigida</i> , and <i>H. jamessi</i>	Painted Desert, Arizona, (<i>jamessi</i>), Mohave Desert (Browning and Monson 1980). Death Valley National Monument Arizona (Ginnett and Douglas 1982).
Grama <i>Bouteloua</i> spp.	Little Harquahala Mountains, Arizona (Krausman et al. 1989, Etchberger 1993). Chihuahuan Desert (Browning and Monson 1980).
Muhly <i>Muhlenbergia</i> spp.	Peloncillo Mountains, New Mexico (Elenowitz 1983).
Needlegrass <i>Stipa</i> spp.	San Andres National Wildlife Refuge, New Mexico (Sandoval 1980). Mohave Desert, Chihuahuan Desert (Browning and Monson 1980).
Ricegrass <i>Oryzopsis hymenoides</i>	Central and southern Nevada (Brown et al. 1977).
Slim Tridens <i>Tridens muticus</i>	Sonoran Desert, Arizona (Browning and Monson 1980).
Squirreltail <i>Sitanion</i> spp.	Central and southern Nevada (Brown et al. 1977).

effort, and food items to achieve compensating effects in time efficiency, cropping rate, bite sizes, and forage quality (Warrick and Krausman 1987, Goodson et al. 1991, Dale and Bailey 1992). As a result of these compensating effects, various combinations of behavior and forage characteristics may produce the same foraging efficiency and the same nutritional status in bighorn. This could account for the observed poor correlation between forage qualities and food habits of desert bighorn (Krausman et al. 1989).

THERMAL COVER

Thermal cover for desert bighorn consists of shade sufficient to protect 1 or more individuals. Large rocks, cliffs of northern aspect, caves, and tree or shrub canopies have been suggested as thermal cover (Simmons 1969, Krausman and Leopold 1986).

Simmons (1969) positively correlated percent time desert bighorn were bedded with wet bulb temperatures and suggested that the presence of thermal cover is an important characteristic of ideal bedding and watering areas. In contrast, Wakeling and Miller (1990) found no significant relationship between

habitat use and thermal cover for desert bighorn. No model of desert bighorn habitat suggests thermal cover as a necessary habitat component.

MINERAL SOURCES

Mineral sources, or "licks," have been suggested as important habitat components on some desert bighorn ranges (Watts and Schemnitz 1985, Holl and Bleich 1987). However, it is unclear if a mineral lick is necessary in desert bighorn habitat (Russo 1956). Elenowitz (1983) suggested that mineral requirements may correlate with compositions of parent rocks. Mineral deficiencies in forage, especially in sodium, calcium, magnesium, phosphorus and trace minerals, have been suggested to explain unusual bighorn behavior such as eating clay and gravel, licking rocks (Mahon 1969, Browning and Monson 1980, Sandoval 1979), and chewing bones (Warrick and Krausman 1986). Watts (1979b) concluded that migration to a mineral lick explained the "unusual" movement patterns of a remnant population in the Big Hatchet Mountains, New Mexico. He suggested that this lick was used primarily to obtain sodium during periods of plant growth, with elevated potassium levels in forage. Holl and Bleich (1987) also found most lick use during periods of plant growth, but suggested that calcium and magnesium attracted desert bighorn to mineral licks in the San Gabriel Mountains, California.

Table 9. Principle or representative forbs consumed by desert bighorn.

Forb	Location and (Reference)
Bedstraw <i>Galium</i> spp.	Little Harquahala Mountains, Arizona (Etchberger 1993).
Borage <i>Borage</i> spp.	Little Harquahala Mountains, Arizona (Etchberger 1993).
Ditaxis <i>Argythamnia neomexicana</i>	Carrizo Canyon, California (Cunningham and Ohmart 1986).
Filaree <i>Erodium</i> spp.	Little Harquahala Mountains, Arizona (Krausman et al. 1989). Mohave Desert, Sonoran Desert (Browning and Monson 1980, Miller and Gaud 1989).
Globemallow <i>Sphaeralcea</i> spp.	San Andres National Wildlife Refuge, New Mexico (Sandoval 1980). Sonoran Desert (Browning and Monson 1980). Carrizo Canyon, California (Cunningham and Ohmart 1986). Virgin Mountains, Arizona, (Smith and Krausman 1987). Bill Williams Mountains, Arizona (Seegmiller and Ohmart 1982).
Indian Wheat <i>Plantago</i> spp.	Sonoran Desert, Arizona (Browning and Monson 1980, Miller and Gaud 1989). Bill Williams Mountains, Arizona (Seegmiller and Ohmart 1982). Virgin Mountains, Arizona (Smith and Krausman 1987).
Lupine <i>Lupine</i> spp.	Little Harquahala Mountains, Arizona (Etchberger 1993).
Milkvetch <i>Astragalus</i> spp.	Aravaipa Canyon, Arizona (Dodd and Brady 1988).
Russian Thistle <i>Salsola kali</i>	Painted Desert, Arizona (Browning and Monson 1980).
Spinflower <i>Chorizanthe brevicornis</i>	Colorado Desert, California (Browning and Monson 1980).

SPACIAL ARRANGEMENT OF HABITAT COMPONENTS

INDIVIDUAL HOME RANGES

Required habitat components (topographic cover, forage, water, and perhaps thermal cover and a mineral source) must occur within the home range of a desert bighorn. Maximum home range size is limited by an animal's cruising ability and varies among individuals and habitat conditions (Bailey 1984). Reported home ranges of several desert bighorn (Table 12) allow inferences about (1) typical

dispersions of the components of desert bighorn habitat, and (2) the maximum dispersion of these components that still allows range occupancy. Based on limited information (Table 12), all habitat components for desert bighorn ewes normally occur within 17-25 contiguous km², and should not be dispersed over more than about 30-35 km². In contrast to ewes, rams travel more widely and their home ranges may be 2-10 times larger (Table 12). Home ranges of both sexes may be most restricted during the

lambing-nonbreeding season (Etchberger 1993).

HERD HOME RANGES

Home ranges of desert bighorn herds consist of overlapping home ranges of individuals (Leslie and Douglas 1979). Consequently, most herd home ranges must contain multiple sets of habitat components. The area of habitat necessary to support a bighorn herd depends upon (1) habitat quality, (2) habitat contiguity, and (3) herd size. Wakelyn (1984:55) reported herd home ranges in relation to herd size for mountain bighorn. Her regression analysis suggests that herds of 100 mountain bighorn range over 100 km²; herds of 150, over 160 km². However, these home ranges were based on very general maps, some ranges contained unused areas, and some herds were migratory. Consequently, habitat quality and contiguity are not considered in Wakelyn's estimates.

Reports of seasonal home ranges of desert bighorn herds are rare. Variation in sizes of herd home ranges have been correlated with water availability and precipitation (Leslie and Douglas 1979).

Smith et al. (1991) suggested that potential transplant sites should be large enough to support minimum viable populations (MVP) of bighorn, and accepted Geist's (1975:105) arbitrary selection of 125 bighorn as an MVP. Others have suggested 50-100 (Berger 1990), 100 (Bur. Land Manage. n.d.:15), and 150 bighorn (Fitzsimmons 1992) as MVP herd sizes. If a goal for herd size, such as MVP, is selected, the necessary area of herd home range may be estimated from average population density. Smith et al. (1991) used this approach, noting that estimates of bighorn population densities depend upon whether only *used* habitat, or some larger area, is considered in calculating average density. They concluded, for herds on the best habitats in the intermountain West, 125 bighorn require at least a 32 km² home range containing at least

Table 10. Principle or representative browse consumed by desert bighorn.

Browse	Location and (Reference)
Blackbrush <i>Coleogyne ramosissima</i>	Painted Desert, Arizona (Browning and Monson 1980). Canyonlands National Park, Utah (Bates and Workman 1983).
California buckwheat <i>Eriogonum fasciculatum</i>	San Gabriel Mountains, California (Perry et al. 1987).
Creosote <i>Larrea divaricata</i>	Bill Williams Mountains, Arizona (Seegmiller and Ohmart 1982).
Desert lavender <i>Hyptis emoryi</i>	Sonoran Desert, Bill Williams Mountains, Arizona (Miller and Gaud 1989, Seegmiller and Ohmart 1982).
Holly-leaved cherry <i>Prunus ilicifolia</i>	San Gabriel Mountains, California (Perry et al. 1987).
Jojoba <i>Simmondsia chinensis</i>	Colorado Desert, Carrizo Canyon, California, Sonoran Desert, Aravaipa Canyon, Arizona (Browning and Monson 1980, Cunningham and Ohmart 1986, Dodd and Brady 1988).
Morman Tea <i>Ephedra</i> spp.	Sonoran Desert (Browning and Monson 1980). Death Valley National Monument, Arizona (Ginnett and Douglas 1982).
Mountain mahogany <i>Cercocarpus</i> spp.	Mohave Desert, California (Browning and Monson 1980). San Andres National Wildlife Refuge, New Mexico (Sandoval 1980). Peloncillo Mountains, New Mexico (Elenowitz 1983). Death Valley National Monument, Arizona (Ginnett and Douglas 1982). San Gabriel Mountains, California (Perry et al. 1987).
Oak <i>Quercus</i> spp.	Peloncillo Mountains, New Mexico (Elenowitz 1983).
Palo verde <i>Cercidium microphyllum</i>	Bill Williams Mountains, Arizona (Seegmiller and Ohmart 1982).
Propeller bush <i>Janusia gracilis</i>	Sonoran Desert, Arizona (Miller and Gaud 1989).
Ratany <i>Krameria</i> spp.	Bill Williams Mountains, Arizona (Seegmiller and Ohmart 1982). Sonoran Desert, Arizona (Miller and Gaud 1989). Little Harquahala Mountains, Arizona (Krausman et al. 1989, Etchberger 1993).
Sagebrush <i>Artemisia tridentata</i>	Mohave Desert, California (Browning and Monson 1980).
Saltbush <i>Atriplex</i> spp.	Mohave Desert, California (Browning and Monson 1980).
Silktassel <i>Garrya</i> spp.	Chihuahuan Desert (Browning and Monson 1980).

Table 10. Continued.

Browse	Location and (Reference)
Silverbush <i>Argythamnia lanceolata</i>	Sonoran Desert, Arizona (Miller and Gaud 1989).
Velvet mesquite <i>Prosopis velutina</i>	Bill Williams Mountains, Arizona (Seegmiller and Ohmart 1982).
White bursage <i>Ambrosia dumosa</i>	Bill Williams Mountains, Arizona (Seegmiller and Ohmart 1982).
White sage <i>Salvia apiana</i>	San Gabriel Mountains, California (Perry et al. 1987).
Winterfat <i>Eurotia lanata</i>	Virgin Mountains, Arizona (Smith and Krausman 1987). Death Valley National Monument, Arizona (Ginnett and Douglas 1982).

17 km² of usable habitat. In contrast, Smith et al. (1991) noted that an estimated average density of bighorn in the Great Basin (1.9/km², Van Dyke et al. 1983) produced a home range size of 65 km² for 125 bighorn. However, where herds are connected by movements of individuals within metapopulations it may be necessary to manage smaller home ranges for satellite and patch herds (Bailey 1992).

GENERAL HABITAT CHARACTERISTICS

VISIBILITY

The predator evasion strategy of bighorn involves visual detection of danger at a distance, visual communication of danger among individuals, and escape to terrain on which bighorn can outmaneuver potential predators (Geist 1971, Risenhoover and Bailey 1980). Visibility is a potentially important characteristic of all components of desert bighorn habitat.

Risenhoover and Bailey (1985) found mountain bighorn preferred vegetation types providing the least visual obstruction in Waterton Canyon, Colorado. They concluded that visibility enhanced "foraging efficiency" (termed foraging "time efficiency" in this text). Hansen (1982) found desert bighorn foraging farther from escape terrain in areas where vegetation was comparatively short and did not obstruct visibility (Table 1). Etchberger et al. (1989) found currently used habitats offered greater visibility than did abandoned habitats.

Two models of desert bighorn habitat directly consider the impact of visual obstruction on habitat quality. Hansen (1980b:328) considers visibility at water sources, while Armentrout and Brigham (1988) also consider visibility at foraging areas and topographic cover. Other models (Holl 1982, Dunn 1991) address visibility indirectly by rating open vegetation types higher than closed types.

Measurement of Visual Obstruction

At least 5 methods may be used to measure visual obstruction in bighorn habitats: (1) percent canopy cover (Holl 1982), (2) mean vegetation height (Hansen 1982), (3) subjective estimation (Risenhoover and Bailey 1985), (4) objective measurement with a "density board" (Gysel and Lyon 1980:316), and (5) computer simulation of vision-obstructing objects (McCarty and Bailey 1992).

SERIAL STAGE

Biotic succession may impact the quality of bighorn habitat by altering the plant species composition, density, and quality on forage areas; and by altering visibility around any of the 5 habitat components. Visibility has been discussed mainly as a function of vegetation height and density (Hansen 1982, Risenhoover et al. 1988). Wakelyn (1984) demonstrated that existing mountain bighorn ranges had relatively more "open, grassy, and rocky habitats" than did historic ranges in Colorado and suggested that biotic succession had reduced visibility. Likewise, desert bighorn have been attracted by the openness and/or forage of recently burned sites (Burger et al. 1983, Etchberger et al. 1989). Two models of desert bighorn habitat (Hansen 1980b:326, Armentrout and Brigham 1988) recognize this temporal aspect of habitat quality.

INTERSPECIES CONFLICTS

Human Conflicts

Human activities in bighorn habitat are highly variable and may have negative, positive, or innocuous effects on desert bighorn or their habitats (Smith and Krausman 1988). Negative and positive effects are frequently cited (Graham 1971, 1980; Ferrier 1974; Golden and Tsukamoto 1980; Wilson et al. 1980; Skiba 1981; Van Dyke et al. 1983; Dobel 1985). Human activities that are innocuous and compatible with desert bighorn have been cited or quantified less frequently. Negative human impacts frequently cited include: habitat requisition or fragmentation by human use and unintentional interference from recreation, intentional harassment, and excessive harvest or poaching (Graham 1980). Positive human effects include: legal protection of habitat, construction and enhancement of water sources, seeding and fertilizing forage areas, removal of vegetation to enhance visibility, and disease intervention (Graf 1980). Most models of desert bighorn habitat consider human presence detrimental to all habitat components.

Defining innocuous human activities and acceptable levels of these activities requires a more precise quantification of bighorn responses than has usually been reported. Bighorn responses to human activity are influenced by: (1) availability of alternative habitat resources away from the disturbance (as opposed to critical or limiting resources, Wilson et al. 1980); (2) degree of habituation to human presence (Geist 1975, Hicks and Elder 1979); (3) hunting pressure (Geist 1975); (4) group size and sex-age composition of the bighorn band encountering the disturbance (Light 1973, Miller and Smith 1985); and (5) security of the bighorn as determined by visibility, presence of escape terrain, and juxtaposition of bighorn, people and escape terrain (Wehausen et al. 1977, Kovach 1979). Bighorn withdrawal from human activity is often interpreted as evidence of a negative impact upon the animals. However, the meaning of avoidance behavior may be ambiguous. If alternative habitat resources are available, avoiding disturbance may be a successful strategy. In contrast, lack of avoidance behavior at a scarce resource may result in negative impacts from elevated stress (DeForge 1981, Miller 1988). King (1985) found that harassed desert bighorn fed less and were more wary than were undisturbed desert bighorn.

Graham (1980) reviewed literature and concluded humans walking alone, on horseback, or in small

Table 11. Principle or representative succulents consumed by desert bighorn.

Succulent	Location and (Reference)
Barrel cactus <i>Ferocactus</i> spp.	Harquahala and Little Harquahala Mountains, Arizona (Krausman et al. 1989).
Mammillaria <i>Mammillaria</i> spp.	Sonoran Desert, Arizona (Miller and Gaud 1989).
Prickly pear <i>Opuntia engelmannii</i>	Chihuahuan Desert, Sonoran Desert (Browning and Monson 1980). Peloncillo Mountains, Big Hatchet Mountains, New Mexico (Elenowitz 1983, Watts 1979a).

groups are not necessarily detrimental, unless harassment is intentional. Recent literature supports this conclusion (Hicks and Elder 1979, Purdy and Shaw 1981, Skiba 1981, Hamilton et al. 1982) although Miller and Smith (1985) reported that bighorn reacted more to people on foot than to parked or moving vehicles or passing aircraft. Off-road vehicles, motor bikes, boats, dogs, low-flying planes, and helicopters may have more severe impacts but are not necessarily detrimental if contact with bighorn is minimized (Graham 1980, Smith and Krausman 1988).

In 2 studies, desert bighorn responded little to fixed-wing aircraft flying >100 m above ground (Krausman and Hervert 1983, Miller and Smith 1985). However, bighorn appear more sensitive to helicopters (Bleich et al. 1990). In mountain bighorn, neither helicopters nor fixed-wing aircraft elicited heart rate responses when aircraft were >400 m away (MacArthur et al. 1982). Stanger et al. (1986) found little impact of river rafters on bighorn behavior in Cataract Canyon, Utah.

Hicks and Elder (1979) concluded that the Mt. Baxter (Sierra Nevada Mountains, California) herd was not declining due to recreational use of the area, but suggested continued restriction of access and increased restrictions on off-trail hiking. Etchberger et al. (1989) correlated distance to human disturbance with habitat abandonment by desert bighorn in the Pusch Ridge Wilderness, Arizona. However, 19 other habitat characteristics also differed between used and abandoned habitats in that study. Graham (1971) correlated habitat abandonment with the abundance of human activity in the San Gabriel Mountains, California. He concluded that desert bighorn abandoned areas along trails, or within sight of a ski area or a cabin, when human activity exceeded 500 visitor days/season (summer or winter). More intensive studies of mountain bighorn have not

Table 12. Reported home range (HR) sizes of desert bighorn.

Location (reference) HR size (km ²)	No. of bighorn (mean)	Season
River Mountains, Nevada (Leslie and Douglas 1979)		
16.9 (± 1.51 SE)	5 ewes	
17.2 (± 4.32 SE)	5 rams	
Colorado National Monument, Colo. (Creeden 1986)		
4.8 (SD = 2.19)	7 newly released ewes	
32.2 (SD = 15.32)	6 established ewes	
Arches National Park, Utah (Haas et al. 1990)		
5.6	4 transplanted ewes	
Southwest Arizona (Scott et al. 1990)		
22 (range: 7-48)	10 ewes	
115 (range: 15-320)	4 rams	
Peloncillo Mountains, New Mexico (Elenowitz 1984)		
9 (± 0.7 SE)	Newly transplanted ewes	
Desert National Wildlife Range, Nevada (Burger et al. 1983)		
22 (18-24)	4 ewes	Aug-Nov
100	1 ram	
Southeast Utah (King and Workman 1983)		
24 (range: 18-39)	7 ewes	
52 (range: 23-106)	5 rams	
Yuma Proving Grounds, Arizona (Ough and de Vos 1984)		
28 (9-67)	5 ewes	
275 (168-441)	4 rams	
Bill Williams Mountains, Arizona (Seegmiller and Ohmart 1981)		
23 (19-27)	2 ewes	Jan-Jun
Little Harquahala Mountains, Arizona (Etchberger 1993)		
28.7 (± 2.8 SE)	29 ewes	Breeding
16.9 (± 2.7 SE)		Nonbreeding
41.1 (± 4.9 SE)	16 rams	Breeding
14.4 (± 3.1 SE)		Nonbreeding

¹See Burger (1985) for comparison of methods used to measure home ranges.

supported this standard and have documented the ability of bighorn to habituate to similar human activities (MacCallum 1988, Jorgenson 1988, Morgantini and Worbets 1988, Morgantini and Mead 1990).

Human presence at water sources may seriously affect bighorn especially if water is scarce (Graham 1980, Smith and Krausman 1988). Changes in drinking behavior due to human activity have been

documented (Campbell and Remington 1979, Leslie and Douglas 1980). Jorgenson (1974) described reduced use of water sources and surrounding areas following frequent vehicle activity. Wilson et al. (1980) recommended no camping within 400 m of desert bighorn water sources.

Bighorn, especially rams, occasionally travel across corridors with relatively unsuitable habitat between mountain ranges (Witham and Smith 1979, Cochran and Smith 1983, Ough and deVos 1984, Scott et al. 1990). These movements may be important for maintaining demographic and genetic benefits of metapopulations (Bailey 1992). Intermountain travels of desert bighorn may follow the shortest routes having the most secure habitat (affording good visibility, with some escape terrain, Ough and deVos 1984). Vegetation may be managed to enhance this security; but other human activities may produce barriers to bighorn movement. Limited information suggests rams, at least, will cross open flats up to 17.5 km (Cochran and Smith 1983), will cross highways and rivers (Schwartz et al. 1986), will use highway underpasses (Witham and Smith 1979), and will negotiate fences of appropriate design (Helvie 1971, Hinckes 1978).

Competition

Potential domestic competitors include: domestic sheep (*Ovis aries*), cattle (*Bos taurus*), domestic goats (*Capra hircus*), and feral and domestic burros (*Equus asinus*) (Jones 1980, Smith and Krausman 1988). Potential wild competitors include: exotic aoudad (Barbary sheep, *Ammotragus lervia*), mouflon sheep (*Ovis musimon*), ibex (*Capra ibex*), Persian wild goats (*Capra aegagrus*), native mule deer (*Odocoileus hemionus*), collared peccary (*Tayassu tajacu*), black tailed jackrabbit (*Lepus californicus*), white winged doves (*Zenaida asiatica*), Gambel's quail (*Callipepla gambelii*), and chukar (*Alectoris chukar*) (Jones 1980, Smith and Krausman 1988). Even bees may compete with desert bighorn for water (Jones

1980).

Foraging and trailing of wild burros, and grazing of cattle on relatively level areas, has altered composition of desert vegetation (Douglas and Norment 1977, Hanley and Brady 1977, Yancey and Douglas 1983, Dodd and Brady 1986). Overlaps of diets, and of habitat use between desert bighorn and wild burro and cattle have been measured (Seegmiller and Ohmart 1981, Ginnett and Douglas 1982, King and

Workman 1984, Cunningham and Ohmart 1986, Dodd and Brady 1986). Simpson et al. (1978) and Seegmiller and Simpson (1979) suggested introduced Barbary sheep may be direct competitors, to the detriment of desert bighorn. Bailey (1980) proposed that Barbary sheep may compete successfully against desert bighorn because they are better adapted to desert environments than are desert bighorn. However, no one has clearly connected a change in population size or productivity of desert bighorn to a change in burro or cattle numbers; and no one has reported interactions of sympatric Barbary sheep and desert bighorn.

Interspecific competition for water is well documented (Sands 1976, McQuivey 1978, Wilson et al. 1980, Jones 1980, Dunn and Douglas 1982). Desert bighorn, especially ewes and juveniles, are often subordinate to larger ungulates at water sources (Jones 1980, Dunn and Douglas 1982).

Disease Transmission

Spraker and Adrian (1990) and Jessup (1985) listed at least 25 diseases that bighorn may obtain from domestic livestock. Of these, at least 14 have been reported in bighorn. The Desert Bighorn Council Technical Staff (1990) suggests that bighorn have not coevolved with many diseases of domestic sheep and have not developed effective immunity. Limited evidence (Jessup 1985:32) indicates that crossbreeding bighorn with other *Ovis* species does not effectively improve immunity in the offspring. Jessup (1985:33) contends that bighorn are more sensitive to common livestock diseases and parasites than are all other North American wild ungulates. Geist (1985:355-356) argues, based on the zoogeographic history of bighorn, that they have little immunity to diseases carried by species that evolved in temperate and tropical climates. In addition, the immune system of bighorn may be compromised by physiological responses to a variety of stressors (DeForge 1981, Miller 1988, Belden et al. 1990).

Domestic Sheep. – Domestic sheep, as sources of pneumonia (and perhaps scabies), are the most serious threat to bighorn. There are 28 reports of declines or dieoffs of bighorn following exposure to domestic sheep (Goodson 1982, Onderka and Wishart 1988, Onderka et al. 1988, Desert Bighorn Council Technical Staff 1990, Foreyt 1990, Callan et al. 1991). Of these, 19 involved free-ranging bighorn herds, 2 involved bighorn in large pens, and 7 involved bighorn exposed to domestic sheep, or to their bacteria, in small pens under controlled conditions. Scabies was implicated in 5 of the 28 incidents (all prior to 1937); pneumonia was implicated in 16; and 7 incidents were unclear. In all 28 cases, bighorn

died while domestic sheep remained healthy. Attempts to identify an organism, particularly a strain of *Pasteurella haemolytica* that is fully correlated with respiratory disease in bighorn or consistently present in domestic sheep and absent in healthy bighorn, have been unsuccessful (Dunbar et al. 1990, Ward et al. 1990). However, based on the numerous dieoffs of bighorn following contact with domestic sheep, the Desert Bighorn Council Technical Staff (1990) recommended that domestic sheep be kept ≥ 13.5 km from bighorn, and that bighorn not be introduced into areas used by domestic sheep within the previous 4 years. These standards appear arbitrary. The potential for contact of desert bighorn with domestic sheep will be influenced by intervening habitat as well as distance (Ough and DeVos 1984). This potential is not always zero, at least for bighorn rams, at a distance of 13.5 km (Table 12, Cochran and Smith 1983).

Domestic Cattle. – In contrast to domestic sheep, impacts of cattle on diseases of bighorn are less clear. Under some conditions, cattle and bighorn have shared ranges, mostly with little overlap in habitat use and without obvious disease events in bighorn (Blood 1961, Lauer and Peek 1976, McCollough 1982, King and Workman 1984, Dodd and Brady 1986, Cunningham and Ohmart 1986). Cattle are not clearly incriminated as the primary source of any all-age bighorn dieoff in the literature (Mouton et al. 1991). However, cattle are a potential source of many bighorn diseases (Jessup 1985, Spraker and Adrian 1990), notably the viruses parainfluenza type-3 (PI-3), bovine respiratory syncytial virus, and blue-tongue. In addition, a *Pasteurella haemolytica* from cattle has been fatal to bighorn (Onderka et al. 1988). Viruses originating in cattle may compromise bighorn immunity to *Pasteurella*, and have been implicated in chronic lamb mortality that can slowly eliminate bighorn herds (DeForge et al. 1981, DeForge and Scott 1982).

The relative success of bighorn on some ranges shared with cattle may be largely due to ecological separation of the species. On shared ranges, bighorn favored steeper slopes, often $>100\%$, while cattle remained mostly on flatter terrain (McCollough 1982, King and Workman 1984, Dodd and Brady 1986, Cunningham and Ohmart 1986). Likewise, Mueggler (1965) found cattle did not forage >469 m up 50% slopes, nor >281 m up 70% slopes; Van Vuren (1982) did not observe cattle on slopes $>30\%$; and Ganskopp and Vavra (1987) found virtually no cattle on slopes $>40\%$. Consequently, the potential for disease transmission between cattle and bighorn may be a function of (1) the degree of interspersation of steep and gentle terrain, and (2) the amount of

contact caused by interspecies sharing of water resources.

Domestic and Feral Goats. – No literature was found linking disease in bighorn to the presence of domestic or feral goats.

Exotic Ungulates. – Little is known of the threat of disease transmission from exotic ungulates to bighorn. Presumably, species closely related to bighorn offer the most risk of disease transmission. In the Tribe *Caprini*, aoudad, mouflon sheep, Siberian ibex and Persian wild goats are closely related exotic species in North American deserts and semi-deserts. Of these species, the diseases of aoudad have received most attention (Allen et al. 1956, Allen 1960, Ogren 1965, Kelly 1966, Pence 1980). Aoudad carry

diseases and parasites potentially transmittable to bighorn. These parasites have not always been abundant in aoudad. However, due to the potential for competition and disease from aoudad, they have been controlled on bighorn ranges (Morrison 1984, 1985). Consequently, the potential for disease interactions between aoudad and bighorn has not been tested empirically.

Three models of desert bighorn habitat recommend isolation of desert bighorn from exotics and domestic livestock as a prophylaxis. Cunningham (1989), and Wakeling and Miller (1990) recommend isolation from all potential disease sources. Armentrout and Brigham (1988) consider only domestic sheep as a disease threat.

DISCUSSION

For wildlife management, habitat requirements of a species may be defined as the set of physical and biotic entities, quantities, and qualities that are necessary for a population to meet management goals. Usually, goals are stability or expansion of the population. Consequently, managers need to know which habitat elements are essential, deleterious, and insignificant.

EVIDENCE AND INFERENCES

Results from several studies must be combined to define habitat elements. There are 2 assumptions inherent in this process: vocabulary, definitions, and methods are similar across studies, and each conclusion is supported by research that is both internally and externally valid. A conclusion is internally valid if, when tested, it is not disproved for the studied population. A conclusion is externally valid if, when tested, it is not disproved to apply to similar populations not actually studied. External validity requires that studied populations be a random sample from all the populations to which conclusions are applied.

Conclusions regarding habitat requirements are more reliable when they are supported by numerous and diverse sources of evidence. Both experimental and observational evidence relate to the habitat requirements of desert bighorn.

Manipulative and "Natural" Experiments

Ideally, conclusions regarding habitat requirements are drawn from experiments in which habitat

elements are manipulated as "treatments," and treatments and controls are replicated and applied randomly. Such rigorous experiments have not been common in wildlife research and management (Romesburg 1981, 1989) although they have been recommended often (Walters and Hilborn 1978; Bailey 1982, 1990; Macnab 1983; Kirby et al. 1992). In less rigorous "natural experiments," biologists have opportunistically measured wildlife responses to uncontrived variation of habitat elements. Natural experiments provide only correlative evidence of habitat requirements because, without experimental control, numerous factors, in addition to the "tested" habitat element, may differ between treatment and control areas or periods. These "lurking variables" (Joiner 1981) may influence wildlife responses, confounding any effects of the tested habitat element. In manipulative experiments, extraneous variables are controlled by replication and randomization.

Often, natural experiments are not replicated. Some are replicated inexactly by >1 researcher when there is similar chance variation of habitat elements in different times or places. Such replications may provide consistent conclusions regarding habitat elements, strengthening these conclusions and providing a degree of external validity. Limitations of this form of replication are (1) methods and definitions may differ across studies; (2) the external populations to which conclusions will apply may be unclear and the studied populations will not be a random sample from any defined set of populations; (3) results of early studies may lead to observer-expectancy bias (Balph and Balph 1983) in later studies; and (4) there is a danger that extraneous variables

will be consistently correlated with the uncontrived, tested habitat elements, producing erroneous conclusions regarding effects of those elements. This latter problem is reduced, but not eliminated, when treatments and controls are assigned at random in manipulative experiments.

Observation

Three types of observational studies have been common in wildlife habitat research: (1) analyses of anatomy, behavior, or physiology from which the adaptive strategies of species have been inferred and related to habitat requirements; (2) studies of habitat use; and (3) studies of habitat preference. Studies of habitat use provide weak inferences regarding habitat requirements because some habitat elements may be used abundantly only because they are numerous. In preference studies, both availability and use of habitat elements are measured. It is assumed that animal preferences have evolved and therefore indicate habitat requirements for reproduction and survival, as components of fitness. Preference studies have characteristics of natural experiments in that used and unused habitat elements vary naturally in the environment.

CHARACTERISTICS OF LITERATURE ON DESERT BIGHORN HABITAT

Since 1980, at least 41 studies providing information on the habitat requirements of desert bighorn were published in professional journals. Most reported on multiple aspects of habitat: 34 related to habitat components, and 15 to habitat characteristics. The Desert Bighorn Council Transactions and the Journal of Wildlife Management were the major publishers, 23 and 7 respectively. At least 8 M.S. theses (3 resulting in journal publication), 2 Ph.D. dissertations (1 resulting in publication), and 2 Wildlife Monographs were completed giving information on habitat requirements.

Three of the 41 studies involved manipulative experiments, but were without random assignments of treatments and controls. No studies addressed random sampling of individuals, or random assignment of radio-collars when used. Most studies (35) involved single-herds, and none state that herds were selected at random. Only 3 studies addressed time of day of sampling of desert bighorn by stratification, and no studies reported random sampling across time of day. Many studies (15) sampled desert bighorn for ≤ 1 year (range, < 1 month to 6 years). Consequently, often (24) data were not stratified by season.

In 18 of the 41 studies, radio-collars were used to locate desert bighorn for sampling (1-30 collars/study). Ewes (141, 64% of 219) were reported radio-collared more frequently than were males (78, 36%). In at least 2 instances the same radio-collared individuals were used for more than 1 study. Most studies (14) reported more observations per ewe than per male.

Survey routes, fecal groups, incidental observation, or bed sites were used to determine habitat use in 21 studies. These methods suffice if routes or plots are randomly located. However, field investigators may have prior impressions of desert bighorn habitat; therefore the potential for expectancy bias is high. Desert bighorn using "unusual" habitats (unusual with respect to prior knowledge) may be neglected in sampling. None of the 21 studies addressed this issue.

Of the 36 studies reporting funding sources, 29 (81%) were funded by > 1 source. Major sources were state game agencies, the U.S. Fish and Wildlife Service, and the U.S. Bureau of Land Management. Multiple sources could reflect insufficient funding, especially during study design. "Add-on" funds, committed after a study has begun, may not be used effectively if a study has already been compromised by limited start-up funds. Multiple funding sources may also reflect limited agency commitments.

Despite these limitations, some has been learned about the habitat requirements of desert bighorn. The reliability of most conclusions depends upon the number and diversity of studies, not upon the rigor or completeness of individual studies. It has been an inefficient process, and several important aspects of desert bighorn habitat remain uncertain. More rigorous and more efficient research will require more commitment to the scientific method with manipulative experiments. This will require stronger leadership at administrative levels of wildlife agencies.

COMPONENTS OF DESERT BIGHORN HABITAT

Consistent or complementary results from many and diverse observational studies provide strong inferences that topographic cover, water, and forage are habitat requirements of desert bighorn. It is not clear that thermal cover or concentrated mineral sources are habitat requirements.

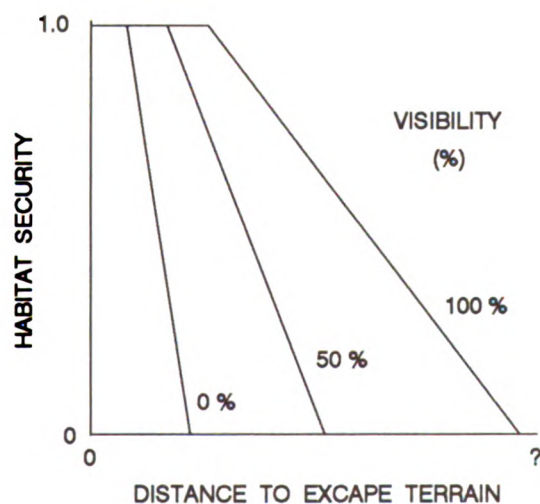
Extreme precision in defining and measuring habitat components may be unnecessary and/or too costly for management purposes. Relatively crude measures of habitat may explain most of the variation in wildlife populations, given the low precision of most population estimates. However, it is appro-

appropriate to investigate the subtleties of wildlife habitat components and characteristics. Research may produce unexpected, but useful and efficient, extensions of habitat definitions and measurements.

Topographic Cover

No definition of escape terrain for bighorn is both precise and widely accepted. A few precise definitions only require a minimum slope steepness (60-100%, Table 3). However, most biologists have defined escape terrain at least partly with descriptions of topographic ruggedness, using terms such as "cliffs," "rock outcrops," and "ravines." These word models allow subjective interpretations, making comparisons among biologists questionable. A widely accepted method for measuring, and therefore defining, ruggedness, is desirable. Dunn (1991) and Beasom et al. (1983) suggested methods that may be used with Geographic Information System (GIS) technology. Ruggedness may be a more important component of escape terrain where slopes are relatively gentle, and less important where slopes are steeper. If ruggedness can be measured, further precision in defining escape terrain may be achieved by investigating these possible interactions of slope steepness and ruggedness.

In addition, visibility and escape terrain interact to provide security for bighorn. Precision in measuring the security value of habitat might be enhanced by investigating this interaction. A precise model of habitat security value might look like:



There is very little information on minimum size requirements for escape terrain, and especially for lambing areas. Proposed standards of 1.6-2 ha (Tilton 1977, Armentrout and Brigham 1988) appear arbitrary, although McCollough's (1982) observations

support them. This should be a profitable area for research.

Protection of bighorn from diseases of domestic cattle appears to depend upon ecological separation of the 2 species, with bighorn using steeper slopes. Unless this hypothesis is rejected, steep slopes are especially desirable for bighorn where cattle are present. When applying habitat models to such areas, model definitions of escape terrain could incorporate especially high requirements for slope steepness. Moreover, bighorn use of relatively gentle slopes may be positively correlated with bighorn population density. It may be useful to investigate effects of bighorn density upon ecological separation from cattle.

Water

Water is the most frequently managed habitat component for desert bighorn. We are discouraged to find only 1 report (Leslie and Douglas 1979) documenting an effect of water development upon the number of sheep. This reflects a widespread need to evaluate activities in bighorn management (Bailey 1990). Biologists should not presume that water is a limiting habitat factor for desert bighorn everywhere, especially in cold deserts and semi-deserts.

Forage

Bighorn are generalist foragers. Consequently, forage is the most complicated and variable habitat component. The values of forage species vary with many interacting factors, including (1) habitat security, (2) seasonal phenology and weather, (3) forage abundance and harvestability, (4) forage chemical/physical composition and palatability, and (5) the diversity and characteristics of other forages on the range. These factors have additional components. Moreover, forage needs vary seasonally, and with the density and sex-age composition of a bighorn herd. With this complexity, it is difficult to predict forage competition from other ungulates, or to predict bighorn responses to forage manipulation.

We found no studies relating forage characteristics to food habits or population performance of desert bighorn. Bighorn can adapt successfully to a great variety of forages. Current knowledge does not justify detailed definitions and measurements of forage resources in habitat evaluations for desert bighorn. Broad definitions of forage value, such as density of grasses = forage value, allow wide geographic application but may provide poor predictions for local populations. Habitat evaluators should develop locally-applicable definitions and scales for rating desert bighorn forages. They should incorporate local, or at least regional, information on food habits, or on preferred foraging habitats.

Thermal Cover and Mineral Licks

Mineral sources, and especially thermal cover, appear to be habitat requirements that are abundant and not limiting on most desert bighorn ranges. Unless local information indicates otherwise, including these habitat components in models of desert bighorn habitat is not justified. If mineral deficiencies are suspected, availability of minerals should be manipulated to test hypotheses that desert bighorn herds are enhanced by this activity.

MINIMUM HABITAT AREA AND MINIMUM VIABLE POPULATION

Spatial requirements for viable bighorn herds and metapopulations should be considered when habitats are evaluated. This requires that goals for bighorn management be developed at a landscape level (Bailey 1992). Metapopulation roles of herds and habitat needs for migration should be considered. Limited information suggests that isolated viable populations of bighorn are at least 100-150 animals and occupy at least 20-65 km² of habitat. Further research on inbreeding and stochastic fade-out in small bighorn populations is needed.

CHARACTERISTICS OF DESERT BIGHORN HABITAT

Evidence presented here justifies inferences that habitat visibility, lack of competition for scarce water sources, segregation from domestic sheep, and freedom from threats of human destruction of habitat are important habitat characteristics for desert bighorn. The importance of other habitat characteristics is either unclear, or may depend upon local conditions. These ambiguous habitat characteristics are seral stage, limited human presence, lack of forage competition, and segregation from the disease threats of domestic and exotic animals other than domestic sheep.

Visibility

The importance of visibility in wild sheep habitat has long been recognized (Murie 1944:104, Hansen 1980b:328, Etchberger et al. 1990) and recent research supports the use of visibility in evaluating all bighorn habitat components. However, attempts to measure visibility in bighorn habitat are recent. Efficient, precise methods are needed. McCarty and Bailey (1992) offer a method for use in pinyon/juniper habitats. Interactions between escape terrain and visibility in providing security for bighorn, and differences in requirements for visibility between rams and ewes, should be investigated.

Seral Stage

There is no evidence that bighorn are limited across their geographic range to either climax or developmental stages of vegetation. Rather, seral stages have been correlated with forage and/or visibility, which can be measured directly in habitat evaluations.

In some areas, habitat evaluators may want to rate open climax habitats higher than open successional habitats. Unlike successional vegetation, open climax vegetation will not require periodic manipulation to maintain openness. Consequently, climax vegetation may be more valuable bighorn habitat because it is less expensive to maintain.

Interspecies Conflicts

Human activities. – As with all wildlife, habitat destruction is predictably detrimental to bighorn. However, bighorn can habituate to a great variety of human activity, when the activity is predictable and non-threatening. Habituation should be facilitated where there is little visual obstruction and bighorn have unimpeded access to escape terrain.

Prudence and the observations of Campbell and Remington (1979), Leslie and Douglas (1980), and Jorgensen (1974) justify limiting human activity at critically scarce water sources. Otherwise, impacts of human activity upon bighorn are difficult to predict. For most bighorn ranges, limiting human activity "to limit stress" is not justified by adequate research. Practical methods for measuring stress are needed, and critical levels of stress are uncertain. However, prudence dictates that all potential stressors be limited on the ranges of bighorn herds that are dangerously small. Otherwise, limiting human activity for securing or enhancing bighorn will be difficult to justify based on the literature reviewed here. Since some herds have habituated to human activity, local data may be needed to incriminate human activity and to justify limiting it. Disqualifying potential transplants because of modest human activity is not justified by the literature.

Managers need information on the willingness and abilities of bighorn to negotiate various types of fences, highway underpasses and overpasses, and other barriers. Observations of bighorn responses to obstacles should be reported and experiments with barriers are needed.

Competition. – Competition for water appears to be a more serious threat to desert bighorn than is competition for forage because (1) mutual use of water resources by sympatric desert bighorn and other ungulates is commonly reported; (2) bighorn have been subordinate to some other species at wa-

ter sources; and (3) water is scarce, and likely to be limiting, on many desert ranges, whereas the limitations of forage are less clear. These reasons justify restricting access of livestock and feral equids to water sources on which desert bighorn depend. Also, in habitat evaluation, lack of competition should be a valuable characteristic of potential water sources.

Much literature contends or implies that many ungulates, including domestic, feral, or exotic species and some wildlife, compete with desert bighorn for forage. Some contentions are deductive inferences from historic declines of bighorn during the late 1800s and early 1900s. However, this evidence is confounded with impacts of diseases and commercial hunting, and is related to extreme levels of domestic grazing. Some contentions are inductive inferences from evidence of overlapping uses of forages, or habitats, by desert bighorn and other ungulates, often from studies of allopatric populations. However, mutual use of resources, even in sympatric populations, does not, by itself, demonstrate competition. Some literature on forage competition with desert bighorn is advocacy - intended to minimize any risks to bighorn. In contrast, there appear to be no documented impacts of forage competition upon desert bighorn populations based upon experimental manipulations of the presence or abundance of po-

tential competitors. Such studies, with controls, randomization, and replication, are needed to clearly demonstrate competition.

Disease. - The threat to bighorn of pneumonia from domestic sheep is well documented in 28 observational and experimental studies. Domestic sheep should be excluded from bighorn ranges wherever possible, and potential bighorn transplant sites should be devalued when domestic sheep are nearby. The risk of desert bighorn contacting "nearby" domestic sheep must be evaluated subjectively according to literature on bighorn movements, the distance of separation, and intervening barriers including lack of escape terrain and areas with poor visibility.

Aside from domestic sheep, transmission of diseases from other ungulates to desert bighorn, especially in field conditions, is documented poorly. Prudent bighorn management will avoid all risks that desert bighorn will contact diseases from other ungulates. However, excluding or removing other ungulates from bighorn range will often be contentious because the evidence incriminating other species as disease sources is scarce or circumstantial. Experiments to clarify the disease threats to bighorn from other ungulates, especially cattle and domestic goats, are needed.

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