THE EFFECTS OF PHYSICAL GEOGRAPHY ON DALL SHEEP HABITAT QUALITY AND HOME RANGE SIZE

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Abstract: Physical geography and prevailing macro-climatic factors determine habitat suitability for Dall sheep (*Ovis dalli*). Dall sheep habitats, which support high densities of sheep, are found on the lee (or snow-shadowed) sides of linearly arrayed mountain ranges which lie across the routes of prevailing bulk air flow. The higher density sheep habitats within these mountains are characterized by long, straight drainages paralleling bulk air flow. These drainages channel cold, heavy, dry air masses downhill after the air masses have cooled and lost the ability to carry water while being forced up and over the mountains. Wind speed increases as gravity accelerates the dense air masses downhill, producing catabatic winds in the absence of (or within) barometric pressure cells. These predictable winds prevent snow accumulation on ridges between tributaries that flow into larger drainages and produce stable wintering habitats for Dall sheep. Habitable but suboptimal ranges are found where one or more of these ideal physiographic conditions is absent and average winter snow accumulation is less than 175 cm (70 in). Winter ranges are less stable in the suboptimal habitats. Preliminary analysis of existing data on Dall sheep movements and home range sizes suggests an inverse relationship between habitat climatic stability and winter home range size. Less stable winter habitats demand greater flexibility in use of available microhabitats by the sheep which occupy these ranges. This demand results in larger home ranges with generally less stable populations of sheep than higher quality (more climatically stable) habitats.

It has been long observed and previously noted (Heimer and Smith 1975, Nichols 1978) that Dall sheep distribution in Alaska is limited by snow accumulation. Dall sheep are not found in areas with mean snow accumulations of greater than 175 cm (70 in) (Heimer and Smith 1975). Heimer and Smith (1975) also speculated that rams harvested from rugged portions of the southern Wrangell Mountains had the highest horn quality index in Alaska because their habitats, unique among Alaska sheep ranges, have southern exposure and are in the snow shadow created by the coastal Chugach Mountains.

It also has been axiomatic that winter winds, along with light, dry snows, are important components of ideal Dall sheep winter range (Nichols 1974, 1978; Heimer 1984). Heimer (1992) argued that, from Dall sheep adaptations, their apparent tendency toward a stable population strategy was an evolutionary result of habitat stability. In this paper we integrate the well-accepted factors of snowfall and wind to form a hypothesis defining habitat quality in terms of the physical geography determining these factors.

BACKGROUND

Why Integrate Prevailing Storm Movement and Geomorphology?

Our interest in the idea that prevailing bulk air (storm) movement is related to Dall sheep ecology through geomorphology resulted from 2 serendipitous events:

Prevailing storm movement. After spending portions of more than 20 winters in classic, high-density Dall sheep habitat in the central Alaska Range, Heimer had the opportunity to work with colleagues from the Bureau of Land Management in a helicopter-supported sheep capture operation in the Tanana/Yukon uplands. Several sheep were to be marked with radiocollars for a movement study. Preliminary studies (Gross 1963) suggested

these Dall sheep moved considerably more than those in other areas (Heimer 1973).

The Tanana/Yukon uplands lie between the Tanana and Yukon Rivers in Interior Alaska. These uplands cannot be accurately defined as mountainous, being primarily rounded hills completely enveloped by boreal forest. Still there are a few scattered hills of montane which support alpine plant communities and reach altitudes of about 2000 m (6000 ft). These mountains are not arrayed as a typical "range of mountains" but scattered discontinuously through-out the lower hills. The Tanana/Yukon uplands are considered the logical refugia of thinhorn sheep during the most recent (Illinoian) glaciation because this area was not glaciated while other current Alaskan sheep habitats were covered by ice (Coulter et al. 1962). As a result of not having been "recently" glaciated, the Tanana/Yukon uplands are atypical of modern Dall sheep country, and call to mind the habitats postulated for mountain sheep as they colonized the new world (Geist 1971, Valdez 1982). The Tanana/Yukon uplands support viable but low-density and disjunct Dall sheep populations which exploit limited "islands" of alpine tundra surrounded by boreal forests. Storm movement through the Tanana/Yukon uplands generally is from south to north, but there is no geographic barrier to eastward (onshore) storm movement into the uplands from the Bering Sea via Norton Sound or the Chukchi Sea via Kotzebue Sound.

In the course of the Tanana/Yukon uplands sheep capture work, Heimer was let out of the helicopter on a mountain top so the helicopter could be maneuvered more safely in pursuit of a sheep. He was told to walk to a more suitable landing area where he would be picked up after the sheep had been caught. In the course of looking for a suitable landing site, Heimer walked eastward along a ridge and noticed that unlike other east-west ridges in the Alaska Range, snow cornices were found on both sides of the ridge. This, of course, meant that snowstorms "blew in" from both sides of that ridge, indicating the absence of a prevailing "windward/leeward" situation.

This situation was strikingly different from the central Alaska Range where an immutable "windward/leeward" snow deposition dominates. There, prevailing bulk air flow is northward up the south slopes, over the top of the Alaska Range, and down the northward drainages into Alaska's Interior region. Thus, air movement results in the "lee" side of east-west ridges being unfailingly on the north side of each ridge. The presence of snow cornices

on both the north and south sides of an east-west ridge in the Tanana/Yukon uplands showed that not all sheep habitats are subject to identical climatic influences with respect to snow and wind direction, and resulted in consideration of differing geomorphic arrangements of high and low density sheep habitats with respect to prevailing bulk air flow.

Geomorphology. The second event was a flight Heimer made from Fairbanks, Alaska to Whitehorse, Yukon in a single-engine Cessna. The flight route was a transect chosen along sheep ranges on the north faces of the Alaska and north slope of the Wrangell Mountains in Alaska, and the south side of the Muskwa trench to Whitehorse in the Yukon. These sheep ranges lie in the precipitation shadows created by the Alaska Range and Wrangell-St Elias Mountains.

Sheep abundance along this transect varies from high in the central Alaska Range and northern Wrangell Mountains to relatively low in the adjacent northern reaches of the St. Elias Mountains of the Yukon. In the course of covering this expanse of sheep habitat along a major sheep population density gradient, it became apparent the high density areas had differing geomorphology than the areas with lower density.

Where Dall sheep populations are at high density, the major drainages are typically oriented north-south (parallel to prevailing bulk air flow), and were generally long and straight. In areas of the Yukon, where sheep density was less, drainages were shorter, more crooked, and flowed "around" the high ridge which forms the southern side of the Muskwa trench. Thus, it seemed unlikely that density driven (catabatic) wind velocity in the Yukon would be as great as in the Alaskan portion of the transect.

Integration and hypothesis. In Dall sheep country, high-density sheep habitats are found along long, straight drainages which lie on the lee sides of linear mountain ranges arrayed perpendicularly to prevailing bulk air flow. In these situations, warm moist air is forced up the windward sides of the mountain ranges where it cools adiabatically causing the water it carries to be deposited as snow. On the south side of the Alaska Range, the ice fields of the West Fork of the Susitna, the Susitna, McLaren, and Black Rapids glaciers attest to this phenomenon.

Once air reaches the crest of the Alaska Range, it is cold, dense, and dry. As this heavy air cascades catabatically down the long, straight drainages characteristic of "classic" Dall sheep

habitat, it removes the typically light, dry snow which accumulates on the lower east-west ridges. These wind-blown ridges support plant communities which form ideal Dall sheep wintering habitats once the snow is removed. In these ideal habitats home ranges are small, and documented fidelity to seasonal ranges is 100% (Heimer 1973, Heimer and Watson 1982, Spiers and Heimer 1990). Stable, high-density populations may be expected in these areas (Heimer 1992).

Our hypothesis predicts where prevailing air flow does not consist of air masses adiabatically cooled to the point of dryness, where the direction of storm front movement is inconsistent, or where geomorphology does not favor acceleration of catabatic winds down relatively long, straight drainage channels to promote wind-scouring of snow from lower elevation vegetated ridges, sheep habitats will be less than ideal. In these marginal habitats, sheep survival should require more adaptive exploitation of micro-habitats. Our hypothesis also predicts a natural consequence of this forced adaptability should be larger home ranges (with increased difficulty for researchers to establish range fidelity) and lower density populations more prone to fluctuation.

METHODS

Optimal ranges with known sheep densities and winter home ranges were identified by the criteria listed above. Optimal ranges in the Alaska (Heimer and Watson 1986) and Brooks Ranges were located on the lee sides of linearly arrayed mountain ranges lying across prevailing bulk air flow routes and having long straight drainages for catabatic air flow.

Two differing types of suboptimal range where density and winter home range data were available also were identified. One range in the Tanana/Yukon uplands was considered suboptimal because it is not arrayed across the path of consistent bulk air flow, and lacks long straight catabatic wind channels. The other suboptimal range was located on the windward (snow depositing) south slope of the Brooks Range. In this area, habitat geomorphology was not unfavorable (the Brooks Range lies across the prevailing south to north bulk air movement). However, snow accumulation approaches the Dall sheep habitability threshold on these ranges because they lie on the south slope of the Brooks Range where snow is deposited.

Overall densities of sheep on each range were determined by dividing population size (from summer aerial count data) by the area counted.

Winter range sizes were determined by monitoring the movements of collared sheep. The greatest linear distance between winter radio-locations was defined as an index of the maximum home range size for each identified winter range. A mean winter range size index for each habitat type was then calculated. In the Alaska Range, 9 optimal winter ranges were identified over the course of 20 years using more than 400 sheep marked with visible neckbands. Range identity and fidelity were then confirmed using radio-marked sheep over separate 3-year periods (Heimer 1973, Heimer and Watson 1986, Spiers and Heimer 1990). In the Brooks Range, 11 optimal ranges were identified by 268 radio locations of 38 sheep over a 5-year sampling period. In the suboptimal ranges of the Tanana/Yukon uplands, 3 winter ranges were delineated by 566 radio locations of 15 marked sheep over a 5-year period (Durtsche et al. 1990). Suboptimal ranges on the south side of the Brooks Range were defined by 82 radiolocations of 12 sheep over a 3-year period.

Fidelity to winter ranges was determined by consistency of range use from year to year. Fidelity was expressed as the percentage of consistent use of winter ranges for marked sheep of each area.

RESULTS

Sheep populations from the "classic" habitats had smaller home ranges and higher population densities than those from "marginal" habitats (Table 1).

DISCUSSION

This paper reports observations which provide a rationalization for long-apparent distributional and population density parameters relating to Dall sheep. It is not a chronicle of experimental science. We have placed our observations in the construct of hypothesis development and testing as a vehicle for their presentation more than as a rigorous hypothesis test. Still, the construct of hypothesis testing provides preliminary assurance that a satisfactory explanation for variations in Dall sheep home range size may be found.

Table 1. Density, winter range size, and observed winter range fidelity by optimal or suboptimal range designation.

Type/Location	Density (sheep/mi²)	Index of maximum winter range diameter	Fidelity (%)
Optimal:			
Brooks Range (north)	2.4 - 5.1	4.0 mi (6.4 km) (n = 11 ranges)	100
Alaska Range*	3.0 - 6.0	5.6 mi (9.0 km) (n = 9 ranges)	100
Suboptimal: Tanana/Yukon uplands[b]	0.2 - 0.5	21.3 mi (34.1 km) (n = 3 ranges)	100
Brooks Range (south)	0.2 - 0.5	5.2 mi (8.3 km) (n = 5 ranges)	81

* Heimer and Watson (1986)
[b] Durtsche et al. (1990)

As suggested by the hypothesis, population densities were higher (approximately 10 times) in optimal habitats than in suboptimal habitats. While no data relating winter forage production per unit of range to Dall sheep density are available, the "optimal" ranges have sustained higher density populations of Dall sheep over time than the "suboptimal" ranges. We suggest prevailing wind and precipitation shadowing are major factors contributing to these sustained high densities because of the consistently greater area of suitable winter range available to sheep.

The hypothesis also predicted correctly with respect to winter range size. Weighted averages of both optimal areas produced a mean maximal winter range index dimension of 7.5 km (4.7 mi) while the weighted average of both suboptimal areas produced a mean maximal winter range index dimension of 17.9 km (11.2 mi).

It is possible this latter dimension could be inflated by data from the Tanana/Yukon uplands. The long time span of data gathering in that area (5 years) and the large number of relocations (566) could have obscured occupancy of smaller discrete ranges if Durtsche et al. (1990) used all locations to define large composite home ranges. If this were the case, actual range fidelity may be lower than the 100% reported from the Tanana/Yukon uplands (Table 1).

Fidelity to defined winter ranges was low in the suboptimal Brooks Range area. Three of 19 marked ewes definitely changed home ranges over the 3 years of the study. These different winter ranges were separated by an average distance of 21.9 km (13.7 mi). It is notable there has been no suggestion of winter range shifting in the optimal areas in either the Brooks Range (n = 38 radio-collared sheep monitored intermittently over 5 years) or Alaska Range (n = more than 400 neckbanded sheep monitored intermittently over 20 years). Still, suboptimal area winter range shifts in the Brooks Range are relatively common. Also in the Brooks Range, Ayers (1986) reported 1 of 10 radio-marked ewes in the Western Brooks Range (which would be classified as suboptimal habitat according to our hypothesis criteria) changed winter ranges between 1983 and 1985. The distance between the centers of her winter ranges was 17.7 km (11.1 mi).

The suggestion that home range size is larger in areas with less-than-ideal geomorphology may be relevant in some management situations. For example, residents of Arctic Village have maintained throughout the last decade that their October subsistence sheep hunting success in the upper East Fork of the Chandalar River (the suboptimal Brooks Range area) has been compromised by aircraft disturbance. The villagers assert that aircraft used by recreational hunters during the August season drove sheep from winter ranges where sheep were successfully harvested during the years before the overflights. This claimed link between presumed aircraft harassment of sheep on their summer ranges and absence of sheep from winter ranges where they were successfully harvested in the past is not credible.

The finding that Dall sheep in this area have large home ranges (particularly if linked to near-threshold snow accumulation because of their range locations on the windward side of the Brooks Range) may explain why sheep have been inconsistently found on the same winter ranges year after year. Similarly, the finding that some Dall sheep home ranges vary tremendously in size obviates concerns that arise when sheep appear to be inconsistent in movements over the short term where habitat geomorphology is not ideal.

Finally, consideration of the geographic or geomorphic correlates of population density and home range size for Dall sheep may be of some benefit to bighorn managers planning transplants. The bighorn literature is replete with accounts of transplants to apparently suitable vegetative communities in suitable proximity to escape terrain, yet the transplants did not thrive. Perhaps a simple overview of prevailing air flow and physiography could serve profitably as a first screen of habitat suitability prior to applying more sophisticated habitat suitability models typically applied in evaluating proposed transplant programs.

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