# **Spatial ecology of desert bighorn sheep (*Ovis canadensis nelsoni*) in the Grand Canyon**

Author: Christian John[1]
[1]Department of Wildlife, Fish, and Conservation Biology, UC Davis

**Introduction**

Bighorn sheep (*Ovis canadensis*) is a group comprised of three subspecies of mountain sheep in North America, including the Rocky Mountain, Desert, and Sierra bighorn (subspecies *canadensis*, *nelsoni*, and *sierrae*, respectively). Bighorn are descendants of the Asiatic snow sheep (*Ovis nivicola*, Geist 1974). Their Pleistocene lineage is cause for controversy, because while some argue that the evolutionary history of desert bighorn indicates they are less well-adapted to arid desert environments than many of the African desert ungulates (Bailey 1980), others argue that the species is a relic laid bare by European-American exploitation (McCutchen 1981). Underlying mechanisms of these conflicting arguments have more recently come to a head, because direct anthropogenic factors and aridification of the US Southwest dually affect the long-term prognosis for desert bighorn populations.

Large mobile organisms respond to environmental variability by segregating their use of space and time according to resources, predators, and social interactions (Brown et al. 1999, Codling et al. 2007, Shepard et al. 2013). Animal movement impacts not only the individual's growth and reproductive success, but also population genetics, biotic community structure, and ecosystem processes (Nathan et al. 2008). By focusing on organism movement, ecologists may learn a lot about how organisms interact with their environments, as well as what indirect effects they have on other members of the community.

The availability of water dramatically affects the way animals use a landscape, especially in arid environments. Animals prioritize their own hydrodynamic requirements over nutritive requirements by staying close to water sources, and minimizing activity during hot parts of the day (McKee et al. 2015). Desert bighorn sheep must consume 4% of their body weight (which in many can approach 175 lbs; Hansen 1965) in water each day to meet homeostatic water requirements (Krausman 1996). Thus, especially during dry times of the year, desert bighorn must maintain a close proximity to springs and rivers. Water, in combination with their proclivity to remain near steep, loose "escape terrain," leaves desert bighorn fairly limited in movement options related to pursuit of forage and evasion of predators when rains are not falling.

The bighorn sheep is an icon of the rugged landscapes characteristic of the American West, especially so in many protected areas such as the Grand Canyon. But, desert bighorn numbers are in decline, and the animals that once numbered in the millions have dwindled to only 25,000 today (Buechner 1960, Gutierrez-Espeleta et al. 2001). Because spatial ecology provides context for the decadal, annual, and sub-annual life histories of species, it is important to understand both long- and short-term processes influencing where and when bighorn distribute themselves regionally and locally. Thus, it is my goal to address three guiding questions: First, what factors control the spatial distribution of desert bighorn? Second, how do desert bighorn seasonally adjust their use of space to compensate for intra-annual environmental variability? And finally, to what extent do natural and anthropogenic forces impact day-to-day movement of desert bighorn? The intent of this discussion centers around bighorn sheep of the Grand Canyon, but data and arguments will be drawn upon from literature that focuses on the desert subspecies (*O. c. nelsoni*) as a whole.

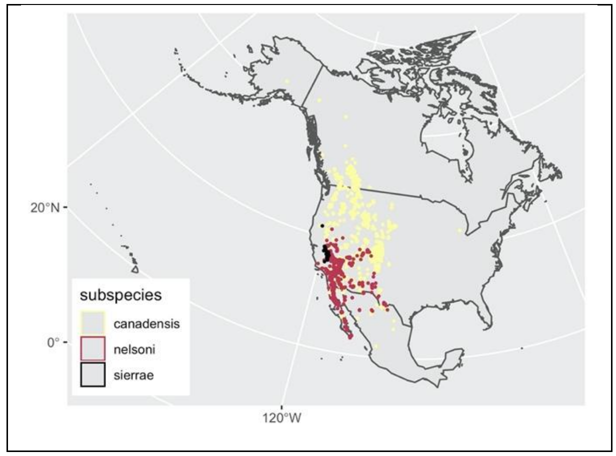


Figure 1. Observations of bighorn sheep (*Ovis canadensis*) submitted to GBIF database. Desert bighorn (*O. c. nelsoni*, red) occupy much of the US southwest and Baja Peninsula of Mexico.

**Distribution**

Bighorn sheep occupy much of the American West, as well as southwest Canada and northwest Mexico (Figure 1). Broadly speaking, bighorn prefer steep mountainous terrain with sufficient open space across which they can detect incoming predators (Geist 1974). They have an incredible thermal tolerance, spanning a range between -55 and 120 degrees Fahrenheit (Cowan 1940).

As a subspecies, the desert bighorn inhabits regions of the US Southwest and northwest Mexico. Although it once inhabited Chihuahua, Coahuila, and Nuevo Leon in Mexico, as well as Colorado and Texas in the US, it was extirpated from those states over the course of the $19^{th}$ and $20^{th}$ centuries. Today, the desert bighorn once again occupies some regions of all but Nuevo Leon thanks to translocation efforts by wildlife managers (Rominger et al. 2004).

In general, bighorn are slow to colonize new areas, or recolonize areas from which they were once extirpated (Geist 1974). They prefer to remain near escape terrain, characterized by steep and often loose slopes (Geist 1974), which can hinder exploratory movements that might otherwise lead to colonization of new habitat by populations (Haughland and Larsen 2004, Stevens et al. 2013). However, significant intermountain movement by desert bighorn is known to occur in spite of the island analogue often assigned to montane environments (Bleich et al. 1990). Today, managed relocation of ungulates is a common practice in the United States, and is an active area of wildlife management efforts to facilitate the long-term persistence of desert bighorn (Singer et al. 2000).

**Seasonal movement**

Large herbivores, particularly in arid environments, depend on precipitation directly due to hydration and thermoregulatory requirements (Grenot 1992), and indirectly due to limiting effects of water on forage availability (McNaughton 1985). The generalization holds true for desert bighorn sheep, which depend heavily on water sources, especially during the hot dry summer (Leslie and Douglas 1980). Total annual precipitation is associated with desert bighorn reproductive success, with higher lamb production in particularly wet years (McKinney et al. 2001). In years with anomalously high rainfall, desert bighorn are able to undergo long-distance movements more frequently; as precipitation conditions change throughout the year, so too do long-distance movements of bighorn (Watts and Schemnitz 1985).

The US Southwest is known for its dry heat – in many cases, mean annual precipitation falls short of a paltry 25 cm (Sheppard et al. 2002). However, spatial variation in the precipitation regime – and particularly high volumes of snow in the Rockies – allow organisms in dry, low-elevation sites to maintain access to fresh water throughout the year. Application of this generalization is hampered by the many dams separating the Grand Canyon from mountainous regions to the north, but because of water flow policies, the pattern still broadly holds true.

Across the Colorado Plateau, precipitation tends to come in the form of frontal rain and snow in the winter months, and brief but dramatic summertime "monsoon" storms (Schwinning et al. 2008). Summer monsoons can substantially supplement wintertime precipitation in some areas (Etheredge et al. 2004). Near the Grand Canyon, summer monsoons contribute about 30% of the annual precipitation.

Bighorn sheep cope with intra-annual variation in temperature by seasonally adjusting the thickness of their coat, growing dense guard hairs in the fall, and shedding hair in large mats in the spring (Geist 1974). Descending from a high-latitude Asiatic sheep (*Ovis nivicola*), the desert bighorn is particularly well-adapted for cold winter months (Cowan 1940). Hot summer months, however, are particularly stressful for them, when they face considerably higher water stress in the absence of standing surface water. For many desert bighorn sheep, the number of natural springs in their home ranges is declining (Longshore et al. 2009b). In one instance, a mass mortality event was documented in which 34 bighorn were found dead in and around a dried spring (Mensch 1969). Desert bighorn have been known to take other steps to fulfill water requirements, such as contending with sharp spines of the barrel cacti to access the juicy succulent's interior (Warrick and Krausman 1989). Some conservation efforts have gone so far as to construct artificial water sources for bighorn that live in protected refuges (Broyles and Cutler 1999, but see Rosenstock et al. 2001). Because of the highly arid summer months, bighorn of the Grand Canyon migrate to the bottom of the canyon during the early spring, and remain in close proximity to the Colorado River throughout the summer (Berger 1977).

**The daily commute**

In the Grand Canyon, temperature variation over the course of a day is dramatic. Daily high and low temperatures can be separated by 20 or even 30°F at a given location (Whitney 1996). In the winter, nighttime lows are frequently in the mid-teens, but occasionally drop below 0°F on the rim of the Canyon. In July, daytime temperatures frequently exceed 100°F in the inner gorge, but only 70-80°F on the rim of the Canyon. Visibility additionally varies, with dark nights leading to impassable terrain conditions when the moon isn't illuminated (Longshore et al. 2009a).

Because bighorn of the Grand Canyon tend to reside at low elevations during the hottest part of the year, they must adjust their daily activity budgets according to diel variation in temperature. Bighorn cope with the intense pressures of high daily temperature and low humidity by adjusting their activity levels throughout the day: when temperatures are high, bighorn activity drops, and when relative humidity increases, so too does activity (Alderman et al. 1989). Bighorn also tend to bed down at night (especially in the hours centered around midnight), leading to a bimodal distribution of activity level, with peak activity during the early morning and evening hours (Alderman et al. 1989). However, this pattern may vary seasonally, with an additional feeding period during midday in the months following the lambing season (Chilelli 1981). Bighorn sheep can be remarkably consistent in their use of time throughout the day: in one study, bighorn groups visited water sources at practically the same time every day, regardless of the sex composition of the group (Whiting et al. 2009).

Day-to-day routine behaviors can be interrupted by predictable, seasonal, and stochastic events. For a few long days every spring, female desert bighorn move to especially high, steep, rugged terrain – habitat where they can safely give birth without concern for predators (Bangs et al. 2005). Although the Colorado River may seem like a formidable barrier to movement, desert bighorn rams have been known to swim across it (Stevens 2012). Instead, most factors impacting day-to-day routine are anthropogenic in nature: hikers, cars, helicopters, and mines all impact the distribution and movement of bighorn sheep. For example, female desert bighorn tend to avoid hiking trails on weekends – coincidental with peaks in human use of those landscapes (Longshore et al. 2013). Desert bighorn also tend to flee farther, and flee for a longer amount of time, when disturbed by hikers than they do when disturbed by vehicles or mountain bikes – a sign that unpredictable hikers, which may approach and/or provoke animals, may incite particularly strong reactions in bighorn (Papouchis et al. 2001). Perhaps the most dramatic factor impacting desert bighorn, particularly in the Grand Canyon, is the sound emanating from tourism helicopters. Helicopters push sound down (as opposed to behind themselves, as in the case of airplanes) due to the physical nature of their rotors, and this loud disturbance has a seasonal effect on bighorn: in the winter, when animals are on the rim of the Canyon, they are much closer to where helicopters fly, and are far less efficient foragers when helicopters come near (Stockwell et al. 1991). Conversely, in the summer when bighorn are nearer the canyon floor, helicopters have less of an effect on foraging efficiency.

## Planning for the future

Across the US Southwest, the climate is shifting toward a more arid regime (Seager et al. 2007). Because precipitation there is so closely linked to the Southern Oscillation, increasingly dramatic El Niño events could lead to increased wintertime precipitation in the Colorado River basin, but stronger La Niña events are expected to have the opposite effect (Hidalgo and Dracup 2003). Since water is already so strong a limiting factor in the southwest, water stress during winters could lead to earlier initiation of downhill migration for desert bighorn in the Grand Canyon.

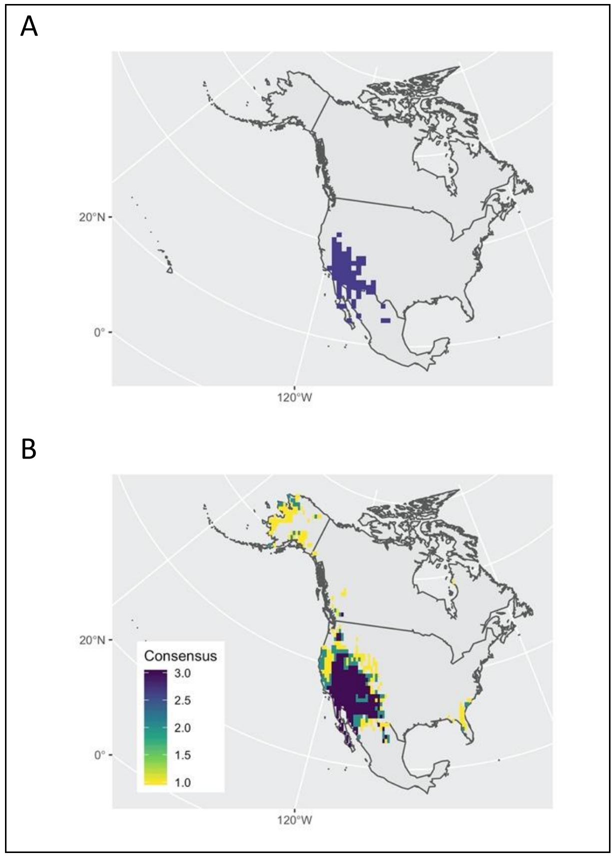


Figure 2. Modeled current distribution (A) and consensus predicted 2070 distribution (B) of desert bighorn sheep, based on AIC-selected generalized linear model. In B, color ramp indicates degree of support across 3 climate models.

To examine the effect of anticipated climate change on the distribution of desert bighorn sheep, I constructed a species distribution model to forecast and map the desert bighorn distribution under a high-emissions warming scenario. I used observations submitted to the Global Biodiversity Information Facility (GBIF.org 2020) to generate a generalized linear model of desert bighorn distribution with respect to broad-scale bioclimatological and topographic characteristics of the landscape they presently occupy (Hijmans et al. 2017). Data were analyzed at 10 degree-minute resolution, and bioclimatological forecasts from the WorldClim V1 dataset (Hijmans et al. 2005) were used to predict the distribution of suitable habitat for desert bighorn in 50 years. I used three CMIP5 models (CNRM-CM5, HadGEM-2, and MIROC5) because they are among the priority models as outlined by the CA Climate Action Team (Pierce et al. 2018), and selected only data for the high-emissions, high-warming RCP 8.5 scenario.

Under the RCP 8.5 scenario, broad-scale environmental conditions that favor occupancy by desert bighorn are not expected to shift dramatically by the year 2070 (Figure 2). In fact, modeled desert bighorn distribution is expected to remain approximately the same as compared to its present spread. Where there is change, it for the most part indicates a broader region will be occupied by desert bighorn in the future. Overall, it seems unlikely that climatic change alone will lead to extirpation of bighorn sheep in the Grand Canyon in the next 5 decades. However, it is important to note that these models ignore land use and landcover, as well as anticipated changes therein over the course of the coming decades. Increased fencing, development of highways, and construction of new pipelines all have the potential to impact movement and dispersal of bighorn across the CO River basin.

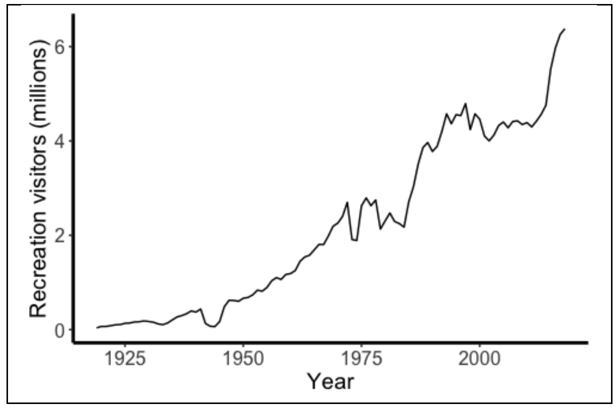

Figure 3. The number of annual visitors (in millions) to Grand Canyon National Park continues to grow (data source: IRMA data portal, US National Park Service).

Furthermore, the number of annual visitors to the Grand Canyon has increased exponentially since the early 20th century (Figure 3), and shows no signs of slowing down. Humans disturb bighorn not just through unpredictable behaviors while hiking (too often, hikers approach wildlife), but also through eruptive sounds arising through conversation and laughter. While the wildlife at many American National Parks is notoriously habituated to the close proximity to humans, human disturbance remains a conservation concern for many species, and a potential danger to park visitors (Geist 2011).

**Conclusions**

Studies of animal movement inform the management and conservation of large mobile organisms by providing land managers with information on distribution information across scales in time and space. For desert bighorn sheep of the Grand Canyon, understanding movement patterns is paramount for allocating grazing allotments, rafting quotas, and park visitor access to different areas. Access to water is of critical importance to inhabitants of arid environments such as the desert southwest, and bighorn in the Grand Canyon seasonally adjust their use of space according to where they can reliably find water. Daily activity patterns seem to reflect a water conservation strategy employed by bighorn, where they increase activity during cooler times during the day, or when the moon is bright enough to support animal navigation. Human activities such as hiking and helicopter flights make the largest impacts on the day-to-day routine of desert bighorn, and should accordingly be monitored and regulated by the appropriate bodies. By educating the public on the status and threats to bighorn sheep, especially in the context of spatial patterns in their seasonal and daily activities, scientists and wildlife managers may help to conserve this iconic subspecies far into the future.

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