Landscape Factors Inhibiting Mountain Goat Movements: A Contribution to Delineating Demographic Units

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ABSTRACT: Because mountain goat (*Oreamnos americanus*) populations are sensitive to anthropogenic mortality, managers of recreational harvests typically restrict hunting opportunity to a small percentage of estimated abundance within some defined boundary (and often, only if abundance meets a defined minimum). In addition to difficulties of estimating abundance in the field, goat managers face uncertainty in geographically delineating where one "population" ends and another begins. Mountain goats typically remain close to steep escape terrain, yet they are sometimes seen in atypical habitats and occasional migrants are known to traverse considerable distances across inhospitable terrain. Molecular approaches provide understanding of barriers to gene flow, but aggregations that can potentially be overexploited likely operate on smaller spatio-temporal scales. Managing a small subset of goats may understate the scale on which demography operates; conversely, managers may face pressure to aggregate units inappropriately. Localized, detailed information to answer these questions are unavailable, and goats exhibit considerable heterogeneity in movement patterns. Thus, we used of GPS-collar data from 184 mountain goats from previous studies in Washington and Montana to quantify movement patterns that may be generalizable across their range south of Alaska. We used U.S. Forest Service digital maps of unconfined valley bottoms (Nagle et al. 2014) as a common currency to quantify goats' willingness to cross atypical habitat, and thus provide a proxy for topography likely to constrain populations at the management scale. As expected, mountain goat movement paths (reflecting ~ 285 goat/years of data) rarely intersected unconfined valleys, particularly those larger than 100 ha in size ($\bar{x}$ = 0.007/goat/year). This suggests that unconfined valleys, as defined, may provide useful surrogates of barriers to movement at the demographic spatio-temporal scale. Such valleys would not appropriately be used directly as demographic unit boundaries, but because they are mapped across the U.S. Northern Rockies can be referenced in assessing if goat hunting boundaries are likely to encompass > 1 demographic unit.

Biennial Symposium of the Northern Wild Sheep and Goat Council 23:12-26; 2022

KEY WORDS: delineating discrete populations, Montana, mountain goats, Washington.

INTRODUCTION

Because of their slow rates of increase, weak responses to reductions in density, and the difficulty of limiting recreational harvest only to males, mountain goat populations are sensitive to anthropogenic mortality (Toweill et al. 2004, Hamel et al. 2006). Indeed, excessive harvest by legally permitted hunters is generally accepted as a primary cause for historic declines in abundance (Mountain Goat Management Team 2010, Rice and Gay 2010). This is particularly true among native populations, albeit somewhat less so among introduced populations (DeCesare and Smith 2018). Mountain goats (goats, hereafter) also face increasing stress from climate change (Pettorelli et al. 2017, White et al. 2018, Sarmento et al. 2019) and, in some areas, changes in the make-up and behavior of their predators (Lehman et al. 2020). That said, goats are classified as a game species in most jurisdictions where they are present, and wildlife agencies and Indian tribes face the challenge of providing hunting opportunity when possible while avoiding overharvest. Indigenous tribes may also wish to pursue customary and traditional consumptive use of goats without inducing population declines (Jessen et al. 2021).

In response, many jurisdictions have adopted generalized guidelines to assist managers in setting harvest quotas. These typically include metrics guiding offtake rate (e.g., proportion of the total population deemed safe to remove annually), as well as minimum abundance at which a population can be considered eligible for recreational harvest (e.g., McDonough and Selinger 2008, Toweill et al 2004, Mountain Goat Management Team, 2010). But even if such metrics are based on rigorously conducted analyses and field surveys, the question often remains as to exactly what geographic areas contain goats that compromise a demographic unit (Caughley 1977), i.e., "a biological unit at the level of ecological integration where it is meaningful to speak of a birth rate, a death rate, a sex ratio and an age structure in describing the properties of the unit." Goat "populations", particularly those inhabiting large blocks of contiguous mountain habitat, can be challenging to identify.

If there are policies for providing hunting opportunity when biologically sustainable, as well as for larger rather than smaller geographic units, how does one know if the search for some number of goats (e.g., 50 or 100) would result in inappropriately aggregating animals that don't actually function as a demographic unit? Conversely, if one assumes that only animals consistently known to be associating with one another can be considered a demographic unit (e.g., Sevigny et al. 2021), would such aggregations overlook demographic connectivity occurring on larger spatio-temporal scales? These characteristics of goat social structure and sensitivity to harvest beg a difficult question: What, in any given geographic area, is the appropriate spatial extent over which it is appropriate to consider that animals share birth and death rates (and thus expect that they will respond somewhat predictably to any given rate of hunting mortality)?

Although it is well established that goats are tightly tied to escape terrain, the advent of GPS collaring and molecular techniques has revealed that goats occasionally make long-distance movements, sometimes crossing atypical habitats (Smith and Raedeke 1982, Rice 2010). An appealing and intuitive response to the question posed above is to capture and place GPS-collars on goats in and near the geographic region of uncertainty and to evaluate potential boundaries delimiting demographic units based on these local data. Although local and updated information is always useful, small sample size may result in overlooking movements that effectively link group of goats. Here we are interested in understanding characteristics of unusual movements that may, despite their rarity, function to link individuals via interbreeding and/or coping with mortality risks sufficiently similar to justify considering them as belonging to a single demographic unit.

Advances in landscape genetics have yielded considerable insight into population structure of goats in specific areas (Shirk et al. 2010, Shafer et al. 2012, Shirk and Cushman 2014, Parks et al. 2015, Wolf et al. 2020, White et al. 2021). When available, this information on gene flow provides valuable insight for population managers, and should be considered.

However, it seems likely that the dynamics that ultimately inform demographic rates operate on shorter-temporal and finer geographic scales than those illuminated by metrics of genetic relatedness (Palsbøl et al. 2006, Lowe and Allendorf 2010). Occasional effective migrations can function to connect aggregations of animals genetically that otherwise cope with different mortality risks, and/or that commonly (if not exclusively) form separate breeding units (Mills and Allendorf 1996, Wang 2004). It would seem quite possible for a manager to inadvertently over-harvest animals if they are incorrectly assumed to be part of a larger group (or a group with higher productivity) even in the absence of any genetic differentiation.

Alternatively, one may gain insight (although not certainty) regarding the likely dynamics among animals in a localized area from any generalizable patterns that are observed consistently in a large sample of animals that may not necessarily be apparent from a small sample from the particular area of interest. In this study, we asked if one or more “common geographic currencies” could be identified that could serve as proxies to the ideal (but unattainable) determinants that serve to differentiate units of animals to which the abstractions of vital rates might usefully apply. A small contribution toward this end may be better understanding movement patterns of individual goats because even if we lack the ability to identify populations we know that they consist, ultimately, of individuals. We know without further examination that most goats stay in relatively small areas most of the time (an important exception being those who travel long distances to mineral licks; Poole et al. 2010, Rice 2010, Kroesen et al. 2020). We also know that -- sometimes - goats (usually but not always young males) make atypical movements, crossing terrain that goats usually avoid. Here we ask if there are patterns we can glean from these movements that would help us answer the question: "What geographic features are likely to delimit goat 'populations' (at the temporal scale relevant to a biologist interested in keeping mortality rates sustainable)"?

Roads used by motorized vehicles are an obvious candidate for such a common currency, and have been implicated as drivers of genetic isolation in both bighorn sheep (*Ovis canadensis*; Epps et al. 2005) and goats (Parks et al. 2015). However heavily travelled roads are rare within most goat habitat, and thus likely to be relatively insensitive barometers of constraints to movements at a fine scale. Thus, we also consider here a metric termed unconfined valleys (Nagle et al. 2014). This metric was developed to aid land managers in understanding ecological processes that may differ depending on valley morphology. Confined valleys are “typically narrow and v-shaped…have relatively steep, erosive gradients, and….little to no floodplain...In contrast, unconfined valleys are wider depositional areas, with extensive alluvial fill and broad floodplains” (Nagle et al. 2014). Although neither the rationale nor algorithm for identifying unconfined valleys have anything to do with goats or their fidelity to escape terrain, we reasoned that such valleys might function as an objective and readily available proxy for landscape features that limit goat movements. Essentially, whereas we typically focus on the steep (and typically locally-highest elevation) areas where goats spend more of their time, here we turn the tables, and focus on the flattest (and typically locally-lowest elevation) areas. Whereas we know that goats can and do descend to move among patches of steep escape terrain, we ask here whether there are landscape features that characterize (or, if possible, even define) areas that goats do not use, and thus may contribute to isolation among aggregations of individuals.

METHODS

We obtained and mapped travel routes of free-ranging goats, using existing data from goats that had been outfitted with GPS collars, regardless of the collars’ fix acquisition frequency. We obtained and mapped both roads ("USA Major Roads", ESRI, Tele Atlas of North America), and unconfined valleys (Nagle et al. 2014; https://www.fs.fed.us/rm/boise/AWAE/projects/valley_confinement.shtml). Using ArcGIS, we then queried each movement path for whether it intersected a road or unconfined valley (and if the latter, the area of the valley intersected). Data came from studies in Washington State (Rice 2008, 2010; Vales et al. 2016; Harris et al. 2022), and Montana (J. Cunningham, Montana Fish, Wildlife and Parks, unpublished; F. Hayes, Colorado State University, unpublished). We defined resident goats as those who had not been translocated (even if their ancestors had been), and introduced goats as those who had earlier been translocated from their natal ranges. We lacked data on ages of goats in the sample, but only a few were younger than 2 years-of-age.

GPS collars were programmed in response to each study's unique objectives. Both Montana studies programmed collars to obtain locations every 4 hours, whereas almost all translocated animals in Washington were programmed to obtain locations every 23 hours (the exception being a handful in the final year of the project programmed to obtain locations every 12 hours). Most collars used in studies by Rice (2008, 2010) were programmed to obtain locations every 3 hours, but some had variable fix schedules depending on season. In all cases, missed fixes resulted in longer achieved intervals between locations than programmed (Table 1). For Montana goat data, we first filtered for data quality, removing all locations with DOP > 2. For Washington data, we removed records for DOP > 4. Additionally, we visually inspected each movement route, and removed clearly anomalous locations that were individual points unaccompanied by any other points anywhere close. For translocated data, we removed all locations < 1 year from the date of release to limit the influence of exploratory movements (e.g., Fryxell et al. 2008, Werdel et al. 2021, Harris et al. 2022 specifically for these animals). Most goats descend to lower elevations in winter and use forested terrain more than in summer (Poole and Heard 2003, Rice 2008), and breeding occurs only during late October—early December, suggesting this time period might best be isolated when examining potential constraints to movement (but see Richard et al. 2014 for an example in which males did not move among previously identified subpopulations). However, the rarity with which goats move away from escape terrain appears similar year-round (Poole and Heard 2003, Rice 2008). We also reasoned that at least some influences on survival (which should be similar among animals constituting a demographic unit) occur year-round. Therefore, all analyses used goat locations year-round.

We characterized goat location paths by 1) gender; 2) whether the goat was resident or introduced to the area (albeit > 1 year earlier); and 3) geographic area (of which there were 4: Glacier Park, Montana; Bridger Mountains Montana; Washington Cascades north of Interstate Highway 90 (I-90, hereafter); and Washington Cascades south of I-90). We also noted some cases in which goats were associated with known mineral licks (Rice 2010, Kroesen et al. 2020).

To determine if any avoidance of unconfined valleys and major roads by goats was not simply an artifact of these features being rare within their overall geographic range (they appeared to be, Figure 1), we created and mapped randomized goat movement paths to act as a null hypothesis for comparison. For each documented movement path of resident (i.e., non-translocated) goats in Washington State, we generated 3 pseudo-paths by offsetting each actual path in a random direction and distance, with the offset distance randomly selected from a normal distribution with standard deviation of 10 km. These 153 paths represented 'goatlike' movement paths within the general area used by each goat (i.e., with the same number, direction, and length of each individual path segment as the actual goat but independent from the underlying

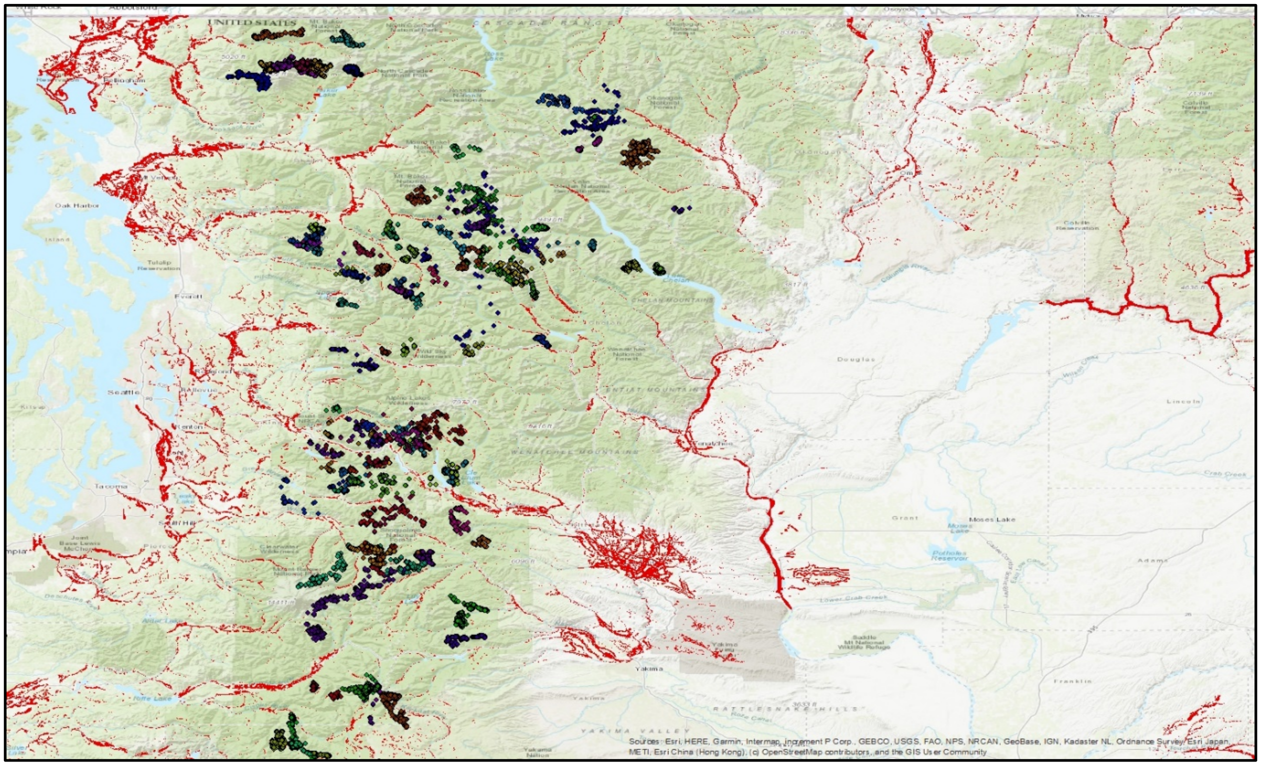


Figure 1. Topographic map of the western Washington, USA, showing locations from GPS-collared mountain goats (dots) and unconfined valleys (Nagle et al. 2014, red polygons).

topography). This analysis was analogous to investigating selection at the 3rd order level given evidence of selection at the 2nd order (*sensu* Johnson 1980). To test whether observed frequencies of unconfined valley and road crossings differed from the crossing frequencies of these random paths (i.e., assumed to quantify the expectation under the null hypothesis of no selection at the finer geographic scale), we used generalized mixed models with both gender and whether the path was north or south of I-90 as interacting fixed covariates, a negative binomial error structure, and individual goat as a random factor (package glmer, R version 4.0.4). To test whether observed and random paths differed in the area of unconfined valleys intersected, we used generalized linear mixed models with Gaussian error structure with goat as a random factor (package lmer, R version 4.0.4.).

RESULTS

Available data

The data set (Table 1) consisted of 184 movement paths from GPS-collared goats, of which 51 (36 ♀,15♂) were residents in Washington's Cascades, 12 (9♀, 3♂) were residents in Montana's Bridger Range, and 24 (19♀, 5♂) were residents captured in Glacier National Park, Montana (together totaling 153.4 goat/years of monitoring;171,575 locations); as well as 97 movement paths of goats (60♀, 37♂) surviving at least one year after having been translocated into Washington's Cascades from the Olympic Mountains and the Elkhorn Mountains in Oregon (representing 130.6 goat/years of monitoring; 36,204 locations).

Crossings of unconfined valleys overall

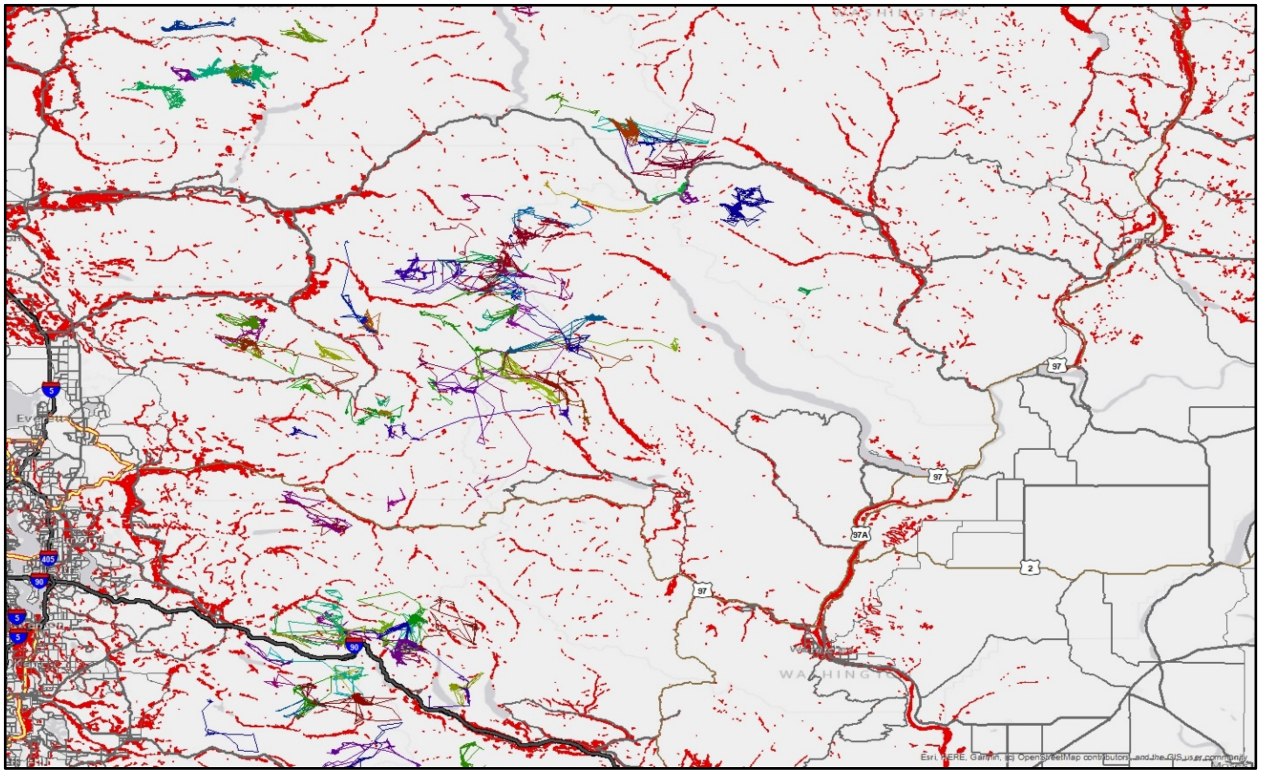
Movement paths of goats generally avoided unconfined valleys and roads (Table 2, Figure 2).

Table 1. Sample sizes of mountain goat movement paths and achieved GPS fix intervals used in the analyses. Region: WA = Washington, N = north of I-90, S = south of I-90, Status; R = resident, T = translocated. Highways include state and US highways.

Region	Status	Females	Males	Years monitored	Path segments	Fix Interval hrs ($\bar{x}, SD$)
WA–N	R	24	3	47.8	35,545	14.8 (7.6)
WA–S	R	13	11	46.9	30,878	16.2 (10.3)
WA–N	T	48	32	103.8	29,013	35.8 (9.7)
WA–S	T	12	5	26.8	7,191	35.5 (15.1)
Bridger	R	9	3	12.9	26,287	4.3 (0.4)
Glacier	R	19	5	45.9	78,865	5.1 (0.4)
TOTAL		125	59	284.1	207,779	

Table 2. Summary of mountain goat movement paths and summaries of unconfined valleys and highways crossed. Region: WA = Washington, N = north of I-90, S = south of I-90, Status; R = resident, T = translocated. Highways include state and US highways.

Region	Status	Valley crossings (all)	Valley Crossings (> 1 km^2)	Valley Crossings (0.5-1 km^2)	Valley Crossings (> 0.25 -0.5 km^2)	Area of valleys crossed ($\bar{x}$)	Highway crossings
WA–N	R	6	0	0	0	0.015	0
WA–S	R	33	0	0	2	0.101	2
WA–N	T	53	2	5	3	0.214	2
WA–S	T	16	0	0	0	0.036	0
Bridger	R	0	0	0	0	0.000	0
Glacier	R	17	0	0	0	0.016	6
TOTAL		123	2	4	4	0.109	10



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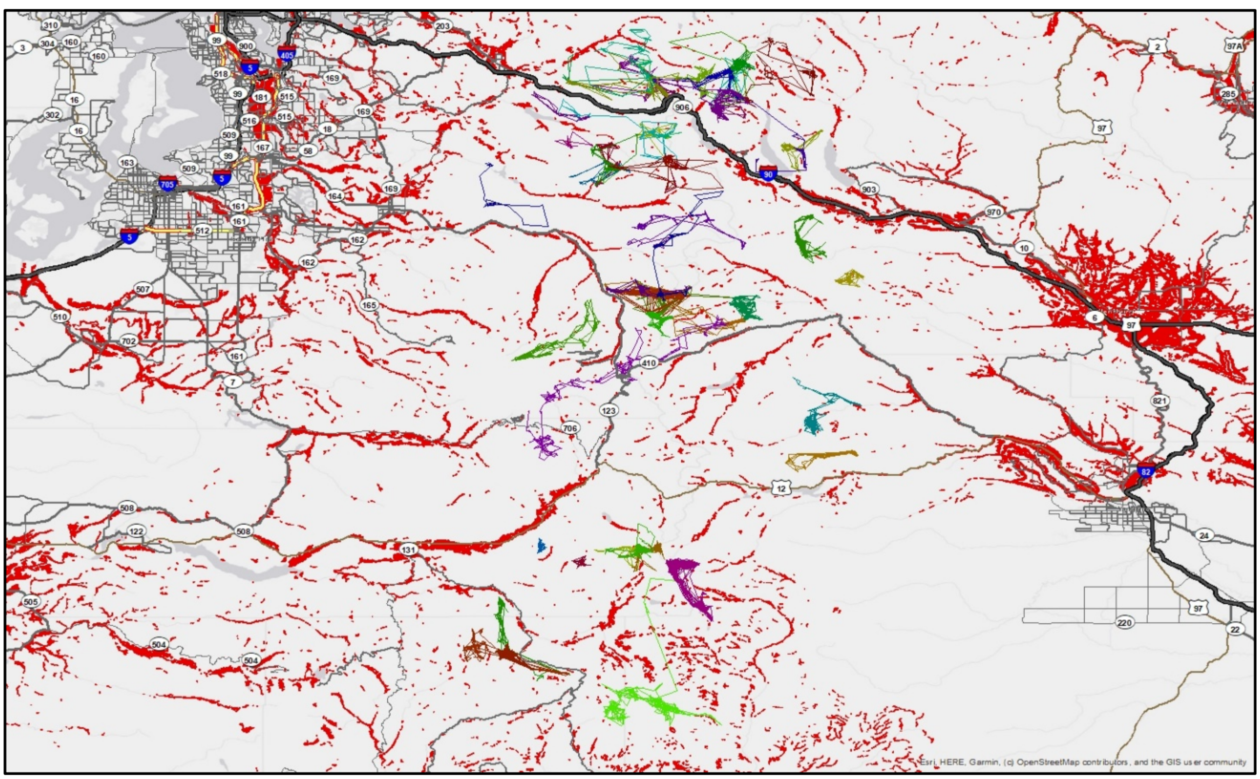

b.

Figure 2. Paths of GPS-collared mountain goats (various colors) and unconfined valleys (red polygons, Nagle et al. 2014) in Washington State, a) north of I-90 and b) south of I-90.

Overall, goats crossed unconfined valleys at a mean rate of 0.441/goat/year. Among all goats, 118 (64%) made no crossings of unconfined valleys and of the 66 that did, only 2 crossed unconfined valleys larger than 1.0 km^2 ($\bar{x}$ = 0.007/goat/year). An additional 5 crossings were of unconfined valleys >0.5 km^2<1.0 km^2 ($\bar{x}$ = 0.018/goat/year), and 6 crossings were of unconfined valleys between 0.25 km^2 and 0.5 km^2 ($\bar{x}$ = 0.021/goat/year). The mean size of unconfined valleys crossed by all goats was 11.4 ha (SD = 56.4 ha, Figure 3).

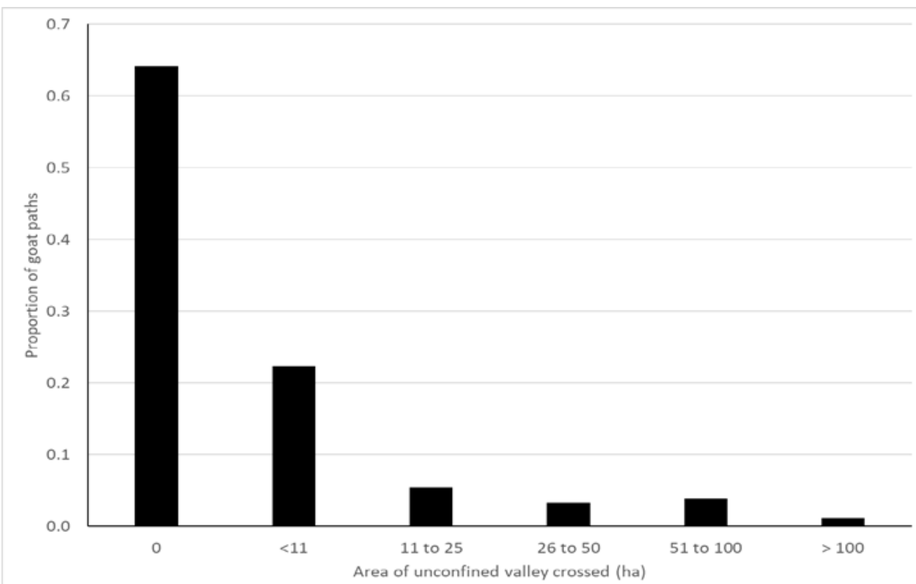

Figure 3. Proportion of unconfined valleys of various sizes (area in ha) crossed by mountain goats monitored by GPS collars. See text for details.

Crossings of highways and other major roads

Crossings of major roads and highways were rare. No goat movement paths crossed I-90 (the only highway of this class within, or adjacent to, the study areas). Washington State Highways 20, 92, 410 and 706 were crossed once each. Four of the 6 goats captured in the southern part of Glacier National Park (near the Walton salt lick) crossed US Highway 2, which has been identified as a partial barrier to movement from grizzly bears (*Ursus arctos*; Waller and Servheen 2005). However, 2 of these 4 appeared to use primarily (and perhaps exclusively) the underpass that was built, in part, to allow goats safe access to the salt lick (Singer and Doherty 1985). Crossings of minor forest roads were not quantified (in some cases, were not mapped), but appeared to be common.

Crossings of unconfined valleys by geography

Examining the geographic origin of the sample more closely, none of the 12 goats monitored in the Bridger Mountains crossed unconfined valleys (habitats used by goats in the Bridgers included none, Figure 4). Among resident goats in Washington, the 23 living in the relatively gentler terrain south of I-90 accounted for 34 of 39 total unconfined valley crossings, whereas only 5 crossings of unconfined valleys were documented from the 28 goats living north of the highway where steep terrain is more contiguous. Among translocated goats, the frequency of unconfined valley crossings among animals south of I-90 was 0.60/goat/year, compared with 0.51/goat/year for animals north of highway. The cumulative area of unconfined valleys crossed by goats north of I-90 (17.11 km^2, 0.16 km^2/goat/year) was larger than among goats living south of the Highway (0.60 km^2, 0.02 km^2/goat/year). However, 10.6 km^2 (> 62%) of the total unconfined valley area crossed by goats north of the Highway was due to just 2 animals (1♀, 1♂), each of which made roundtrips across narrow sections of linear (but large) unconfined valleys (Figure 5). Were these 2 movement paths to be considered outliers and redacted, total areas of unconfined valley crossed/goat/year by goats north of the Highway

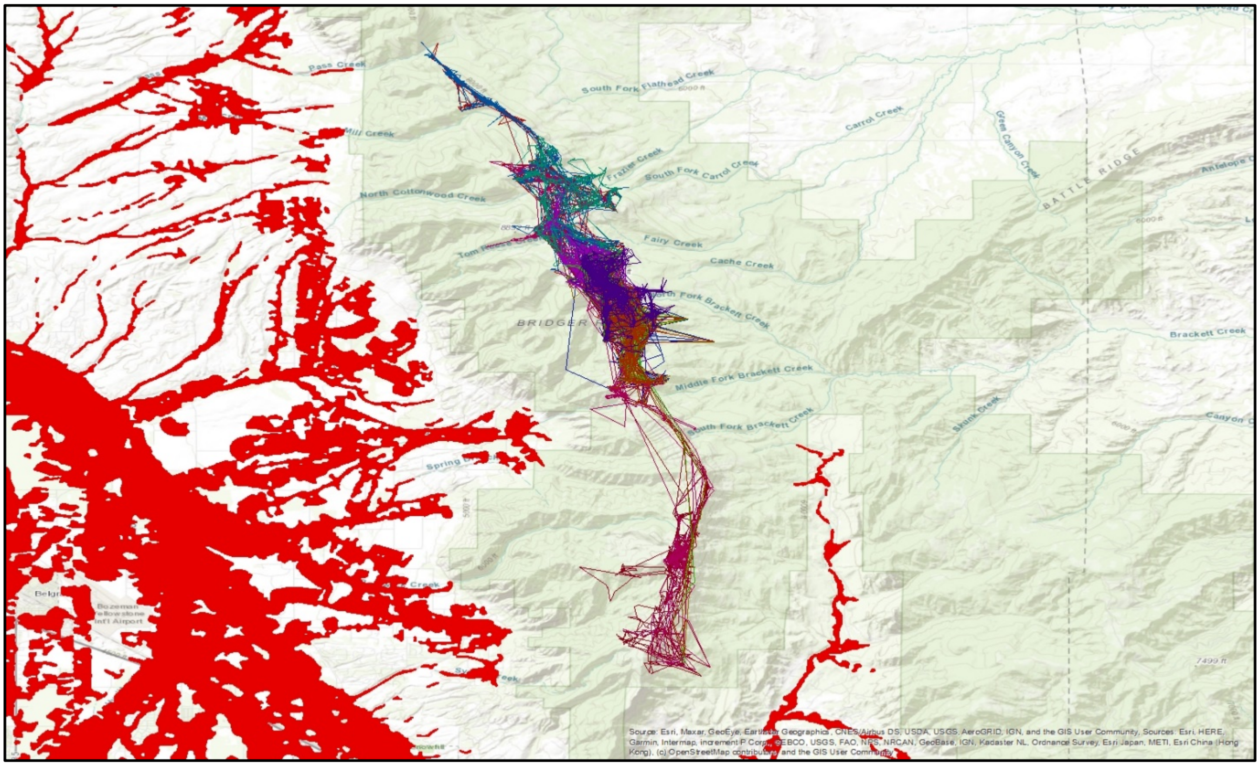

Figure 4. Movement paths of GPS-collared mountain goats (various colors) in the Bridger Mountains, SW Montana. Unconfined valleys (Nagle et al. 2014) in red polygons.

(6.55 km^2, 0.07/goat/year) was closer to the value observed among goats south of the Highway. The 24 goats captured in Glacier National Park (4 of which also used adjacent portions of the Flathead National Forest) accounted for 17 unconfined valley crossings, but the valleys crossed tended to be small ($\bar{x}$ = 1.6 ha). Small sample size prohibited testing whether goats known to use salt licks differed in frequency of crossing valleys or roads from those with unknown lick use (although most appeared, qualitatively, to travel extensively to and from lick sites).

Crossings by gender and residency status

Movement paths of males were more likely to cross unconfined valleys (0.78/goat/year) than females (0.30/goat/year; see Appendix for statistical support). Data did not support there being a gender difference in likelihood of crossing highways or major roads. Crossings of unconfined valleys by translocated goats (0.53/goat/year) did not differ significantly from crossings by resident goats (0.36/goat/year; see Appendix).

Observed vs. random paths (null model)

Actual goat paths crossed unconfined valleys less frequently than randomized paths (Table 3), both in a model paired with I-90 (random path = 1.827, SE = 0.397, z = 4.598, P < 0.001; south of I-90 = 1.597, SE = 0.502, z = 3.183, P = 0.001, interaction not significant), and in a model paired with gender (random path = 1.303, SE = 0.265, z = 4.917, P < 0.001; male = 1.328, SE = 0.471, z = 3.109, P = 0.002, interaction not significant). In examining only large (i.e., area > 1 km^2) unconfined valleys, actual goat paths were even less likely to cross than random goat paths (random path = 21.503, SE = 1.303, z = 16.509, P < 0.001; south of I-90 = 1.013, SE = 4.257, z = 0.238, ns; interaction not significant), and paths of males crossed these

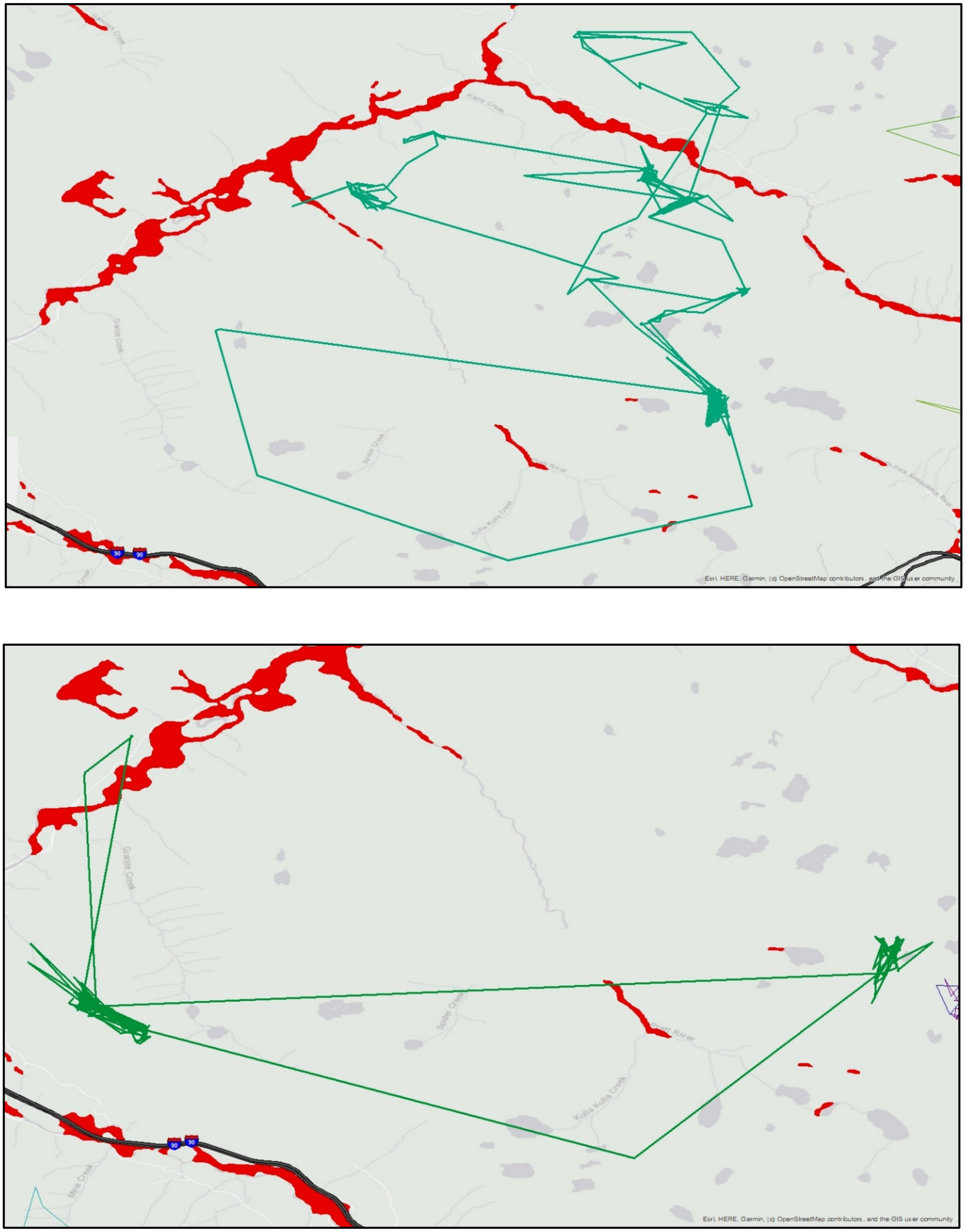

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Figure 5. Movement paths of 2 mountain goats wearing GPS collars that crossed large (1 km^2) unconfined valleys, exceptions to the finding of this investigation that such crossings were rarely observed. Both panels A and B depict the area just north of I-90 in the Snoqualmie River drainage.

Table 3. Summary statistics of observed movement paths of resident mountain goats in Washington State (*n* = 51) and randomized versions of these paths (*n* = 153), showing mean and standard errors of number of crossings of unconfined valleys, number of crossings of large (>1-km^2) unconfined valleys, number of crossings of important local roads, and number of crossings of state highways.

Crossings	**Observed movement paths**	**Random movement paths**
Mean (SE) unconfined valley crossings	0.76 (0.21)	2.56 (0.26)
Mean (SE) large (> 1-km^2) unconfined valley crossings	0.00 (0.00)	0.31 (0.05)
Mean (SE) important local road crossings	0.02 (0.02)	0.11 (0.03)
Mean (SE) state highway crossings	0.02 (0.02)	0.16 (0.03)

large valleys more frequently than those of females (random path = 1.153, SE = 0.295, z = 4.917, $P < 0.001$; male = 1.328, SE = 0.427, z = 3.109, $P = 0.002$; interaction not significant). Results (not shown) were similar when examining paths crossing important roads and state highways. (US highways and were not crossed frequently enough for meaningful analyses).

DISCUSSION

Examining a large data set created by combining goat movement paths from different research projects in diverse geographic settings yielded some important insights. Importantly, although some goats traveled considerable distances (and even occasionally emigrated from their place of birth to other goat habitat separated by areas devoid of escape terrain), they rarely crossed large-sized valley bottoms or heavily-used highways to do so. Although narrow, steep-sided valleys did not necessarily inhibit frequent goat movements, broad valleys were very rarely traversed (and when goats moved to steeper terrain on either side of broad valleys, they did so by going around them). This finding is unsurprising, as it confirms and reinforces goats' well-accepted characteristic of fidelity to steep escape terrain (Shafer et al. 2012, Wolf et al. 2020). Mapping it in this way, however, allows one to clearly visualize not only places goats will use, but also places they will not use, even in the absence of site-specific or genetic data.

A plausible interpretation is that this exercise has taught us nothing more than that goats inhabit mountainous terrain where flat valleys larger than a few hectares are rarely found in any case. However, the finding that observed movement paths were significantly less likely to cross large valleys than movement paths randomly drawn from within their mountain habitats suggests that goats make conscious choices to avoid those few valleys they could potentially cross while moving among safe foraging and resting locations.

Considering goats' infrequent use of broad valleys leads to some nuance in interpreting the isolation among goat populations associated with heavily used highways (Shirk et al. 2010, Parks et al. 2015). Although it is likely that motorized traffic (or possibly associated fencing) directly inhibits highway crossing, major highways in this study were generally associated with large unconfined valleys that were avoided whether or not they contained highways. Thus, goats may have had two reasons for hesitancy in crossing highways: 1) traffic disturbance itself, and 2) tendency to be located relatively far from steep terrain. This suggests that crossing structures built to encourage connecting genetically-isolated populations may be unsuccessful if built where the inherent topography discourages goat use.

There may be other, better proxies than unconfined valleys, as defined and mapped by Nagle et al (2014) to predict obstructions to free movement of goats. Advantages of this metric are that is objective, well-documented, and already mapped for almost all goat habitat in the contiguous U.S. states (Washington, Oregon, Idaho, Montana, and northwestern Wyoming). The published algorithm should allow for similar mapping and use elsewhere.

MANANGEMENT IMPLICATIONS

Neither unconfined valleys nor major roads, by themselves, provide sufficient information to demarcate the boundaries of demographic units for goats; at best, they provide insight and can function as part of a comprehensive assessment incorporating locally-unique factors. It would be simplistic (and probably unfeasible) for mangers to use either unconfined valleys or major roads as sole criteria for demarcating population boundaries. Because some landscapes evidently allow goats to circumvent rather than travel through broad valleys, the mere presence of an unconfined valley does not provide an unambiguous signal indicating where demographic connectivity is lacking. By the same token, our data would not support the inference that the lack of an unconfined valley guarantees demographic connectivity. That said, these results suggest that although goats occasionally move through terrain lacking escape terrain, they very rarely cross large valleys or major roads to do so. Thus, we recommend that managers uncertain about the validity of assumed goat population units examine maps with that include both these features. Where extensive areas of unconfined valleys occur within a region considered contain a single demographic unit, additional consideration should be given to the possibility that goats separated by them may interact with one another too rarely to function as a single unit.

ACKNOWLEDGEMENTS

Additional data from GPS-collared goats was graciously provided by Jennifer Sevigny (Stillaguamish Tribe), Mike Sevigny (Tulalip Tribe), Mike Wolton (Sauk-Suiattle Tribe), Julie Cunningham and Kelly Proffitt. Geographic Information System assistance was provide by Smith Wells (MFWP). Special thanks to Josh Greenberg, Washington Department of Ecology. Thanks also to K. McDonald, J. Gude, for supporting this effort, and to N. DeCesare for adding insight into this line of inquiry as well as improving the manuscript.

APPENDIX

Because the sample of goat movement paths was not a random sample of the universe of possible paths that might inform extrapolation to unstudied areas, we examined simple models to see if crossings and/or area crossed differed by gender, region, or resident vs. translocated goats. Important differences among these factors would suggest caution in extrapolating the summary results and inferences from this study. Conversely, few, or minor differences would suggest that the sample used was a reasonable surrogate for a truly random sample from all goats to which inference might be applied (which, needless to add, would be nearly impossible to obtain).

To this end, we developed general linear models (glm) with candidate predictors gender, region (WA N, WA S, Glacier, Bridgers), resident vs. translocated, and mean fix interval of each goat path, weighted by the number of years monitored. For models examining frequency of crossings per goat, we assumed a negative binomial error structure; for models examining the dependent variable area crossed (a continuous variable), we assumed a Gaussian (normal) error structure. We compared models with all reasonable combinations of predictor variables using AIC, and considered predictors significant at $\alpha = 0.05$.

In univariate analyses of crossing frequency, we found no effect of residency, region, or mean fix interval at the nominal level of significance. However, there was evidence that gender affected unconfined valley crossing frequency (male effect = 0.831, SE = 0.248, $t = 3.224$, $P = 0.001$). In univariate analysis of area of unconfined valleys crossed, no predictors were significant at the nominal level. In multivariate models of unconfined valley crossing frequency, almost all AIC model weight was taken by the top model, which included effects of residency, region, gender, and mean fix interval. However, in this top model, only gender (as in the univariate model) and mean fix interval (interval = 0.019, SE = 0.009, $z = 2.171$, $P = 0.030$) were significant. In multivariate models of area of unconfined valley crossed, the model with both gender and residence was the top AIC model, but neither predictor was significant at the nominal level.

In summary, these results provided some assurance that the general results found in the body of the paper (i.e., that unconfined valleys are crossed rarely, that large unconfined valleys are crossed extremely rarely, that interstate highways are almost never crossed, and the US and other high-use highways are very rarely crossed) are not highly dependent on characteristics of the (non-random) sample used. The only strong effect found was that males cross valleys more readily than females, but the ratio of > 1-year old females to males in the sample (~ 2:1) is probably not greatly different from that found in most unsampled free-ranging populations. Thus, our sample is probably a reasonable reflection that males are more willing to cross these valleys than females. We also found some indication that GPS fix frequency affected valley crossing frequency, with movement paths connecting fixes further in time from each other more likely to cross an unconfined valleys than paths connecting fixes obtained in closer temporal sequence. This suggests that some mapped valley crossings may have been artifacts of missed data fixes (i.e., animals may have avoided these valleys, but a straight line connecting two locations many hours apart resulted in a valley intersection). This effect renders our conclusions conservative. That is, goats with no history of having been translocated will cross unconfined valleys and highways somewhat less frequently than indicated by the sample in this study taken as a whole.

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