Sighting Probability and Survival in Two Colorado Bighorn Sheep Herds

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ABSTRACT The management of many bighorn sheep (*Ovis canadensis*) herds in Colorado is based primarily on the results of annual surveys that provide data on minimum population sizes and demographic rates. Very little information is available on bighorn sighting probability during these surveys, which prevents the derivation of population estimates with known levels of precision. To refine the management of the Georgetown and Pikes Peak bighorn herds and to inform the management of other herds, we initiated population estimation and demographic studies on both of these herds. From 2005-2009, we captured and radio-collared 73 bighorn sheep from the Georgetown herd (49 ewes, 24 rams) and 54 bighorn sheep from the Pikes Peak herd (32 ewes, 18 rams). During the summers of 2006-2009 in the Georgetown herd and 2007-2009 in the Pikes Peak herd, we conducted mark-resight studies to estimate adult ewe and ram population size and sighting probability. We also estimated annual survival rates for ewes and rams in each herd. We then incorporated these data into population models for each herd. The July adult population estimates ranged from 342 (SE = 42) to 445 (SE = 50) for Georgetown and from 92 (SE = 5) to 142 (SE = 7) for Pikes Peak. The mean proportion of the modeled population observed during surveys was 0.35 in the Georgetown herd and 0.48 in the Pikes Peak herd. In the Georgetown herd, the mean annual survival rate excluding harvest was 0.91 (range 0.85-0.97) for adult ewes and 0.92 (range 0.85-1.0) for adult rams. For Pikes Peak, the mean annual survival was 0.90 (range 0.88-0.92) for adult ewes and 0.90 (range 0.81-1.0) for adult rams. The leading cause of adult mortality was vehicle collisions in the Georgetown herd and mountain lion (*Puma concolor*) predation in the Pikes Peak herd.

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KEY WORDS bighorn sheep, Bowden's Estimator, Colorado, Georgetown, mark-resight, *Ovis canadensis*, Pikes Peak, population estimation, sighting probability, survival.

The management of many bighorn sheep (*Ovis canadensis*) herds in Colorado is based primarily on the results of ground or helicopter surveys (George et al. 2009). More than 25 years of ground survey results in the Georgetown and Pikes Peak herds have provided valuable information on sex and age ratios, minimum population size, and minimum

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distributions (Huwer 2010, 2015, Stiver 2011). These surveys do not provide information on bighorn sighting probability, which prevents the derivation of population estimates with estimates of precision (Anderson 2001, Pierce et al. 2012). To refine management of the Georgetown and Pikes Peak herds and to inform the management of other herds, we used mark-resight methods to estimate the population size and demographic parameters of both herds. The objectives of these studies were to 1) estimate the size of the populations with statistical confidence; 2) determine adult ewe and ram sighting probability during surveys; 3) estimate survival rates for adult ewes and rams; 4) develop a population model for each herd; and 5) determine the proportion of the modeled populations observed during surveys of each herd.

STUDY AREA

The Georgetown bighorn sheep herd occupied 330 km^2 west of Denver, Colorado (Fig. 1). During the summer, the bighorn sheep are found throughout this overall range. Elevation ranged from 1,700 m to 4,000 m. The climate varied greatly from east to west depending on elevation. The eastern, low-elevation portion had comparatively warm summers and mild winters. The western, high-elevation portion was much colder with snow covering timbered areas and north-facing slopes from November through May.

Vegetation was diverse depending on elevation and climate. Foothills shrubs dominated to approximately 2,300 m. Mountain riparian communities were found along streams, wetlands, and irrigation ditches between 1,700 m and 3,400 m. Ponderosa pine (*Pinus ponderosa*) dominated communities were found up to 2,500 m with Douglas fir (*Pseudotsuga menziesii*) covering many north-facing slopes in the foothills. Subalpine forests occurred from 2,500 m to timberline at approximately 3,500 m. Within the subalpine forest zone, lodgepole pine (*Pinus contorta*) intermixed with aspen (*Populus tremuloides*) dominated sites up to 3,200 m. Engelmann spruce (*Picea engelmannii*) and subalpine fir (*Abies lasiocarpa*) forests interspersed with meadows were dominant to timberline. Stands of limber (*Pinus flexilis*) and bristlecone pine (*Pinus aristata*) also occurred at higher elevations. Alpine tundra, alpine willows (*Salix* spp.), and rock dominated above timberline.

The Georgetown herd is a native population. It was supplemented with 47 bighorn sheep from the Tarryall herd of Colorado in the 1940s. Numbers fluctuated from less than 50 before supplementation to nearly 500 in 2001. During this study, 300-400 bighorn sheep occupied the area making

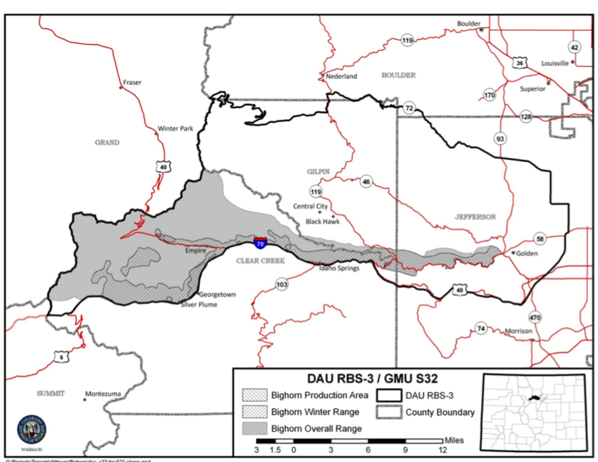

Figure 1: Location of the Georgetown bighorn sheep herd.

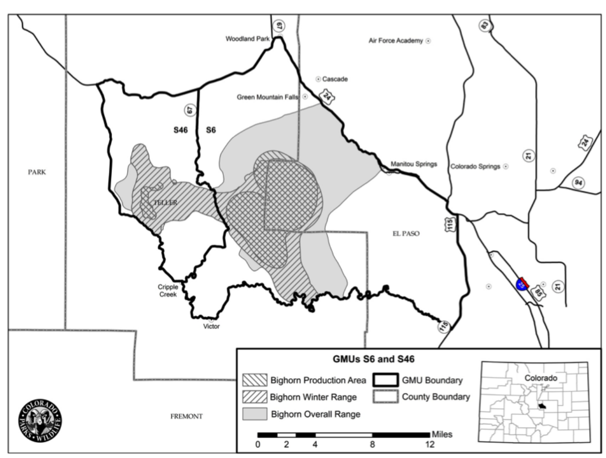

Figure 2. Location of the Pikes Peak bighorn sheep herd.

it one of the largest bighorn sheep populations in Colorado. Potential predators of this herd include mountain lions (*Puma concolor*), coyotes (*Canis latrans*), bobcats (*Lynx rufus*), domestic dogs (*Canis lupus familiaris*), golden eagles (*Aquila chrysaetos*), and black bears (*Ursus americanus*). Several major highways and heavily used roads, including Interstate 70, US Highways 6 and 40, State Highway 119, and the Central City Parkway, run through the range of the Georgetown herd. Many of these roads bisect traditional movement corridors. The Georgetown herd was contained within Data Analysis Unit RBS-3 and Game Management Unit (GMU) S32 (Huwer 2010).

The Pikes Peak bighorn sheep occupied 250 km^2 west of Colorado Springs, Colorado (Fig. 2). During the summer, the bighorn sheep occupied 109 km^2 of summer range, which was comprised primarily of alpine areas where visibility is high. Elevation ranged from 2,500 m to 4,300 m. Climate conditions varied depending on elevation. The highest mean snowfall occurred in March and April but snow was possible at higher elevations throughout the year. Weather in the Pikes Peak herd was characteristic of high elevation peaks throughout Colorado. During the summer, conditions were relatively mild during the morning hours but thunderstorms often formed during the afternoon. Snow and freezing temperatures were possible throughout the year. During the winter and spring, strong winds (>100 knots) were common at the summit.

Vegetation was diverse depending on elevation and climate. Above timberline (> 3,500 m), the vegetation communities were typical of alpine bedrock, scree, and tundra. However, some meadow complexes occurred within the alpine in the Pikes Peak herd. Subalpine communities were composed of Engelmann spruce and subalpine fir, bristlecone, and lodgepole pine; aspen forests occurred between 3,200 m and 3,500 m. Below 3,200 m, much of the area was dominated by ponderosa pine and aspen forests, though some areas contained wet meadow complexes.

The Pikes Peak herd is a native population that has never been supplemented. Numbers have fluctuated from less than 40 in the 1950s to an estimate of 425 in the 1990s. It was thought to be one of the largest bighorn sheep herds in Colorado at the start of this study. Potential predators of this herd include mountain lions, coyotes, bobcats, golden eagles, and black bears. No major highways pass through the range of the Pikes Peak herd. The Pikes Peak herd is contained within Data Analysis Unit RBS-8, GMU S6 (Pikes Peak) and GMU S46 (Dome Rock, Stiver 2011).

METHODS

From 2005 to 2009, we deployed radio collars on 73 bighorn sheep (49 ewes, 24 rams) in the Georgetown herd with adherence to the Colorado Bighorn Sheep Capture and Translocation Guidelines (George et al. 2008). We captured these bighorn on winter range throughout the study area via drop netting (11 ewes, 4 rams), chemical immobilization (28 ewes and 8 rams), and helicopter net-gunning (10 ewes, 12 rams). We used 3 types of radio collars: 1) Lotek LMRT-4 (very high frequency (VHF) collars; 46 ewes and 23 rams); 2) Lotek Global Positioning System (GPS) 3300SL (store-on-board GPS collars; 2 ewe and 2 ram); 3) and Northstar Globalstar D-cell (GPS collars with satellite upload; 9 ewes). We recaptured 9 of the bighorn sheep originally given VHF collars to replace the collars with Lotek GPS collars (1 ewe and 1 ram) and Globalstar collars (7 ewes). In the Pikes Peak herd, we deployed radio collars on 50 bighorn sheep (32 ewes, 18 rams). We captured these bighorn on winter range throughout the study area via drop netting (6 ewes, 5 rams), chemical immobilization (13 ewes and 9 rams), clover trapping (7 ewes), and helicopter net-gunning (5 ewes, 5 rams). All Pikes Peak bighorn sheep were collared with VHF Lotek LMRT-4 radio collars. We affixed unique alphanumeric marks to the collars in both study areas to enable individual identification, as required by mark-resight methodology (Bowden and Kufeld 1995, Thompson et al. 1998, Pierce et al. 2012).

In the Georgetown herd, each July from 2006-2009, we conducted 5-7 one-day resight surveys. Each survey consisted of 11-16 ground-based routes conducted simultaneously either on foot or from trucks or off-highway vehicles. The total combined length of all the routes was 298 km. These routes were designed to provide maximum coverage of the range of the herd and to minimize double counting of bighorn. Routes had been modified and refined during the previous 18 years of July surveys of the area. To determine the proportion of the summer bighorn habitat visible from the resight survey routes of each study area, we used a Geographic Information System (GIS) to conduct a viewshed analysis (ArcMap 10.1, Environmental Systems Research Institute, Inc., Redlands, CA). We derived the viewshed from the 30 m digital elevation model with the Viewshed and Raster Calculator tools in the Spatial Analyst extension.

Observers on each route began at approximately sunrise and continued until completed (3-12 hours later depending on the route). Along each route, 1-6 observers (including CPW staff and volunteers) used binoculars and spotting scopes to find groups of bighorn sheep. The observers recorded the following for each group of bighorn: 1) number of bighorn, 2) classification of each bighorn (i.e., full-curl ram, 7/8-curl ram, 3/4-curl ram, 5/8-curl ram, 1/2-curl ram, ewe, yearling ram, yearling ewe, lamb, or unclassified), 3) number of marked ewes, 4) number of marked rams, 5) mark identifications, 6) behavior, and 7) location. We removed duplicate sightings made during each one-day survey. Using the same methods for the Pikes Peak herd, we conducted surveys consisting of 9-11 routes from 2007-2009. Each survey was repeated 7 times in 2007 and 6 times in 2008-2009 in July and August. The total combined length of routes was 62 km. For the Georgetown herd, additional resight data were collected via opportunistic sightings and extra routes conducted between complete surveys. Prior to the resight surveys each year, we confirmed that all marked bighorn were within the study areas and alive via ground and aerial radio-telemetry.

Following McClintock and White (2007), we used Bowden's estimator (Bowden and Kufeld 1995) implemented in NOREMARK software (White 1996) to generate a mark-resight estimate with standard errors and 95% confidence interval for each bighorn sheep population. This method assumes that: 1) the sample of marked individuals is drawn from a closed population; 2) each individual has an equal chance of being marked; 3) marked and unmarked individuals are identified and counted correctly; and 4) marking does not increase the probability that an individual is sighted. Additionally, this method allows for mortality during the sighting period. This estimator was appropriate for our sample because it accounted for 1) variation in individual sighting probabilities and 2) resighting of individuals known to be marked but who cannot be identified. Besides mark-resight population estimates, statistical analyses were preformed in R version 3.0.2 (R Core Team 2013) with package nlme (Pinheiro et al. 2014).

One assumption of Bowden's estimator is that the each animal has an equal chance of being selected for marking and that the marked animals are independent. This assumption can be approximated if the selection of animals to be marked is different than the selection of those resighted (White and Shenk 2001). This was achieved in this study by marking animals on winter range and resighting them on summer range. In the Georgetown herd, ground surveys were also conducted during December of each year. Each single-day survey consisted of 5-6 simultaneous routes repeated up to 4 times. We did not use these surveys to produce a December population estimate because the assumptions of Bowden's estimator were likely violated. We did use these surveys to calculate demographic rates and to evaluate differences between July and December surveys.

We calculated the annual individual sighting probability of each marked bighorn by dividing the number of surveys during which an individual was observed by the number of surveys completed each year. We used repeated measures ANOVA to evaluate the interaction between sex and annual sighting probabilities. The mean individual sighting probability does not incorporate collars that are observed but not individually identified. To incorporate these unidentified collars, we calculated the proportion of marked ewes and rams observed on each survey by dividing the number of marks observed by the number of marks in the population. We also compared the number of ewes, rams, and total bighorn observed during each survey to the modeled numbers in the population.

We monitored the radio-collars via ground and aerial radio-telemetry throughout the year. All collars were equipped with mortality sensors except the Globalstar collars; we determined the mortality status of the bighorn wearing these collars by monitoring daily satellite uploaded locations. We located mortalities as soon as possible and, when possible, determined the cause of death. For each herd, we calculated annual survival rates for adult ewes and adult rams from December 2005 to December 2009 using a Kaplan-Meier staggered entry design. Harvest mortality was incorporated separately from natural mortality in the population models described below. Therefore, harvest mortalities were censored when calculating survival rates. This also allows for the comparison of survival rates in Georgetown and Pikes Peak herds to other herds with different harvest pressures.

We developed a population model for each herd to estimate the July and December populations from 1991 to present for Georgetown and from 1988 to present for Pikes Peak (White and Lubow 2002). These optimized fit models incorporated all available Bowden's ewe and ram population estimates; observed December age ratios; observed December sex ratios; observed adult ewe and ram survival rates; and removals via hunter harvest, translocations, and vehicle collisions. Akaike Information Criterion model selection was not performed due to insufficient data.

These studies followed guidelines and protocols approved through the Colorado Parks and Wildlife Animal Care and Use Committee (10-2006, 04-2007 and 07-2006).

RESULTS

Surveys and Sighting Probability

Based on the viewshed analysis, 87% (288 km^2) and 79% (86 km^2) of the area classified as summer bighorn sheep range of the Georgetown and Pikes Peak herds, respectively, were visible from the resight survey routes.

From 2006-2009, we successfully completed 22 resight surveys in the month of July for the Georgetown herd. Two marked ewes were out of the study area in July 2006 and were, therefore, censored from the analysis. One survey in 2006 was not completed due to restricted visibility and one survey in 2007 was excluded from survey averages due to the small number of bighorn observed. From 2007 to 2009, 19 surveys were successfully completed of the Pikes Peak herd.

Within each herd and year, the individual surveys varied widely in the number of bighorn observed; observed sex and age ratios; the individual sighting probabilities of marked bighorn; and the proportion of marked animals observed on surveys. The individual sighting probability of collared animals and the proportion of collared animals observed on surveys were consistently higher in the Pikes Peak herd than in the Georgetown herd (Table 1).

Population Estimates

For both herds, we found an interaction between sex and annual sighting probabilities (repeated measures ANOVA: Pikes Peak T_{52} = 3.944, P = 0.0004; Georgetown T_{128} = 2.152, P = 0.03), so we generated separate estimates for rams and ewes in each herd. The Bowden population estimates in the Georgetown herd ranged from 150 (SE = 19) to 229 (SE = 32) for ewes and from 157 (SE = 37) to 216 (SE = 38) for rams. Based on these estimates a mean of 18% of the ewe population and 9% of the ram population was marked during the resight surveys (Table 2). In the Pikes Peak herd, the Bowden population estimates ranged from 60 (SE = 3) to 92 (SE = 5) for ewes and from 32 (SE = 4) to 50 (SE = 4) for rams. Based on these estimates, a mean of 31% of the ewe population and 28% of the ram population was marked during the resight surveys (Table 3). The 95 percent confidence interval lengths were smaller for the Pikes Peak herd estimates than for those of the Georgetown herd.

Survival

In the Georgetown herd, mean annual survival excluding harvest was 0.91 for adult ewes and 0.92 for adult rams (Table 4). For the Pikes Peak herd, the mean annual survival was 0.90 for adult ewes and 0.90 for adult rams. From December 2005 to April 2011, 37 marked

Table 1. Identification rates and sighting probability (mean and range) of ewe and ram collars during resight surveys in the Georgetown and Pikes Peak bighorn sheep herds, Colorado, 2006-2009.

	Bighorn Sheep Herd						
	Georgetown Herd				Pikes Peak Herd		
	2006	2007	2008	2009	2007	2008	2009
Ewe							
Collars deployed in study area	33	33	33	34	19	22	27
Identified collar observations	61	33	42	38	52	60	93
Unidentified collar observations	4	15	12	15	19	12	6
Mean sighting probability	0.31	0.17	0.25	0.22	0.31	0.45	0.57
Range sighting probabilities	0.00-0.67	0.00-0.67	0.00-0.80	0.00-0.60	0.14-0.57	0.00-0.83	0.00-0.83
Mean proportion of collars observed	0.33	0.24	0.33	0.31	0.36	0.55	0.61
Range proportion of collars observed	0.12-0.45	0.12-0.36	0.15-0.58	0.18-0.47	0.16-0.74	0.41-0.73	0.33-0.81
Ram							
Collars deployed in study area	14	18	16	15	7	11	14
Identified collar observations	26	18	9	7	33	40	29
Unidentified collar observations	2	11	7	8	4	3	3
Mean sighting probability	0.31	0.17	0.11	0.09	0.51	0.61	0.35
Range sighting probability	0.00-0.83	0.00-0.50	0.00-0.40	0.00-0.40	0.29-0.71	0.17-0.83	0.17-0.83
Mean proportion of collars observed	0.35	0.27	0.20	0.20	0.59	0.64	0.38
Range proportion of collars observed	0.14-0.57	0.00-0.50	0.00-0.38	0.13-0.37	0.14-1.00	0.27-1.00	0.21-0.57

Table 2. July population estimates with 95% confidence intervals (95% CI) and percent confidence interval lengths (% CIL) and the proportion of the ewe and ram population that were marked each year in the Georgetown bighorn sheep herd, Colorado, USA, 2006-2009.

Year	Ewe	95% CI	% CIL	Ram	95% CI	% CIL	Prop Ewes marked	Prop Rams marked
2006	174	147-207	34	194	144-261	60	0.19	0.07
2007	229	175-300	55	216	154-303	69	0.14	0.08
2008	185	150-229	43	157	101-245	92	0.18	0.10
2009	150	118-192	49	171	112-264	89	0.23	0.09

Table 3. July population estimates with 95% confidence intervals (95% CI) and percent confidence interval lengths (% CIL) and the proportion of the ewe and ram population that were marked each year in the Pikes Peak bighorn sheep herd, Colorado, USA, 2006-2009.

Year	Ewe	95% CI	% CIL	Ram	95% CI	% CIL	Prop Ewes marked	Prop Rams marked
2007	92	83-103	22	50	43-59	32	0.21	0.14
2008	85	71-104	39	42	34-51	40	0.26	0.26
2009	60	54-67	22	32	25-41	50	0.45	0.44

bighorn sheep (24 ewes, 13 rams) from the Georgetown herd died. The largest source of mortality for ewes was vehicle collisions (11) followed by hunter harvest (3). Other known causes of mortality in the Georgetown herd included mountain lion (2), fence entanglements (1), natural causes (1), liver tumors (1), and hardware disease (1, Fig. 3). For rams, the largest source of mortality was hunter harvest (6) followed by vehicle collisions (3). Other known causes of mortality in the Georgetown herd included mountain lion (1) and wounding loss (1, Fig. 3). From December 2006-April 2011, 19 marked bighorn sheep (10 ewes, 9 rams) from the Pikes Peak herd died. The largest known source of mortality for ewes was mountain lions (3) followed by falls (2, Fig. 4). The largest sources of mortality for rams were hunter harvest (3) and mountain lions (3) followed by falls (2, Fig. 4).

Population Models

From 2006-2009, in the Georgetown herd, the mean proportion of the modeled ewe and ram population observed during a survey was 0.34 and 0.32, respectively (Fig. 5, Fig. 6). In the Pikes Peak herd, the mean proportion of the modeled population observed during a survey

Table 4. Annual (Dec to Dec) survival rates with 95% confidence intervals of adult ewes and adult rams in the Georgetown and Pikes Peak bighorn sheep herds, Colorado, USA, Dec 2006-Dec 2009. Harvested animals were censored.

	Ewe Survival		Ram Survival	
Year	Georgetown	Pikes Peak	Georgetown	Pikes Peak
2005-2006	0.97 (0.92-1.00)		0.94 (0.81-1.00)	
2006-2007	0.85 (0.73-0.96)	0.89 (0.77-0.99)	1.00 (1.00-1.00)	0.88 (0.67-1.00)
2007-2008	0.87 (0.76-0.98)	0.91 (0.85-1.00)	0.89 (0.74-1.00)	0.81 (0.59-1.00)
2008-2009	0.94 (0.85-1.00)	0.89 (0.85-1.00)	0.85 (0.65-1.00)	1.00 (1.00-1.00)
Average	0.91	0.90	0.92	0.90

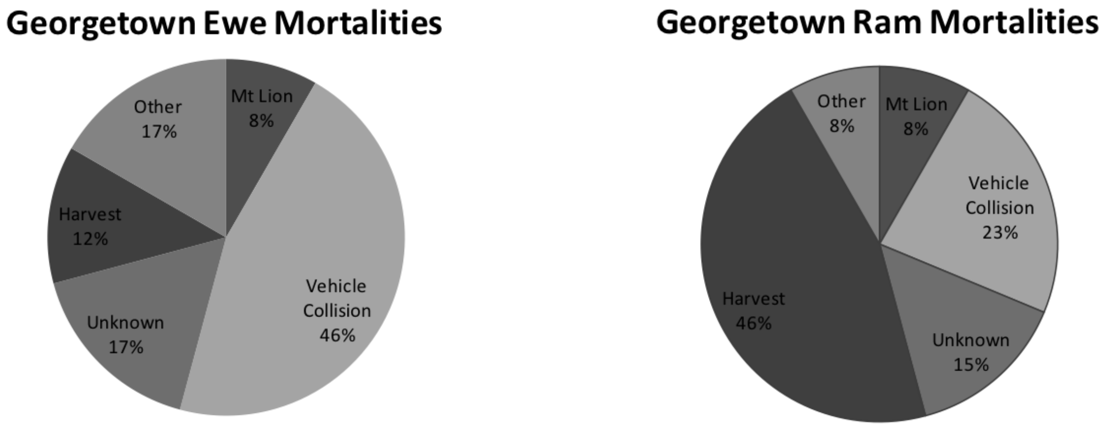

Figure 3. Causes of mortality for the 24 collared ewes and 13 collared rams that died from the Georgetown bighorn sheep herd, Colorado, USA, Dec 2005 - April 2011.

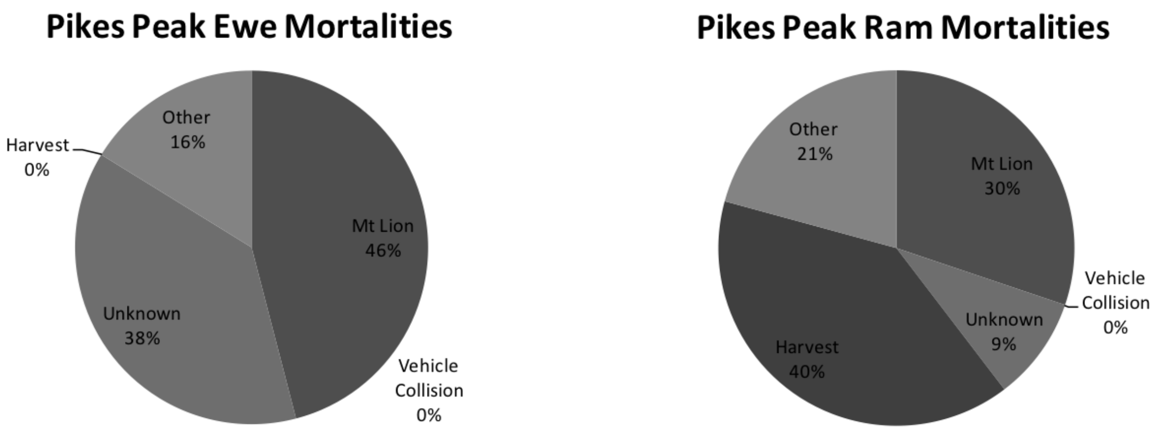

Figure 4. Causes of mortality for the 10 collared ewes and 9 collared rams that died from the Pikes Peak bighorn sheep herd, Colorado, USA, Dec 2006 - April 2011.

from 2007-2009 was 0.52 for ewes and 0.53 for rams (Fig. 7, Fig. 8).

From 1992 to 2010, in the Georgetown herd, a higher proportion of the total modeled population was observed during December surveys (mean = 0.50) than during July surveys (mean = 0.35, Fig. 9). The mean proportion of the modeled population observed during surveys in the Pikes Peak herd was 0.48.

DISCUSSION

We found high variability in mean individual sighting probability between the surveys conducted in the Georgetown and Pikes Peak herds, as well as between years and individual surveys within each area. Although the proportion of the summer bighorn habitat visible from the resight survey routes was higher in the Georgetown study area than in the Pikes Peak study area, the mean sighting probability was consistently higher for the Pikes Peak herd than the Georgetown herd. This was due to several factors. The Pikes Peak herd occupies a smaller area that is primarily alpine where visibility is high. In addition to the alpine, the Georgetown herd occupies forested areas with reduced visibility. Also, survey routes on Pikes Peak were shorter and more easily accessible than Georgetown routes, providing observers with more time each day to survey visible bighorn habitat.

Within each year, sighting probability likely

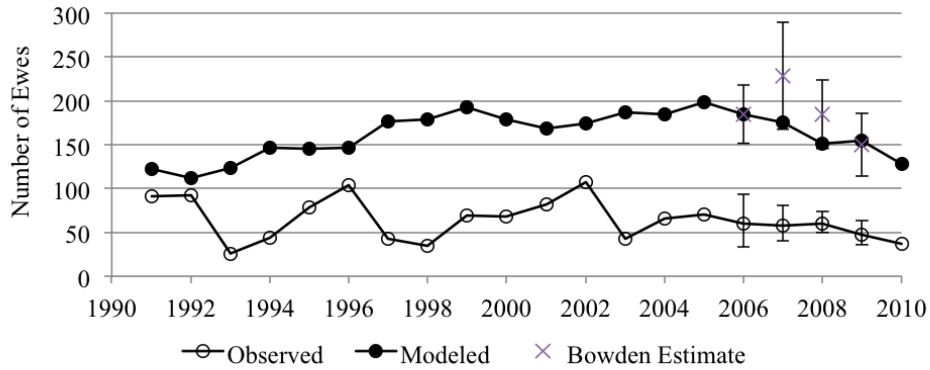

Figure 5. Number of ewes observed during the July survey of the Georgetown bighorn sheep herd, Colorado, 1991-2010; the modeled ewe population for the same time period and the Bowden population estimate with 95% confidence intervals from the mark-resight study 2006-2009. For years in which multiple surveys were conducted, the mean and range of the number of bighorn observed over all the surveys is shown.

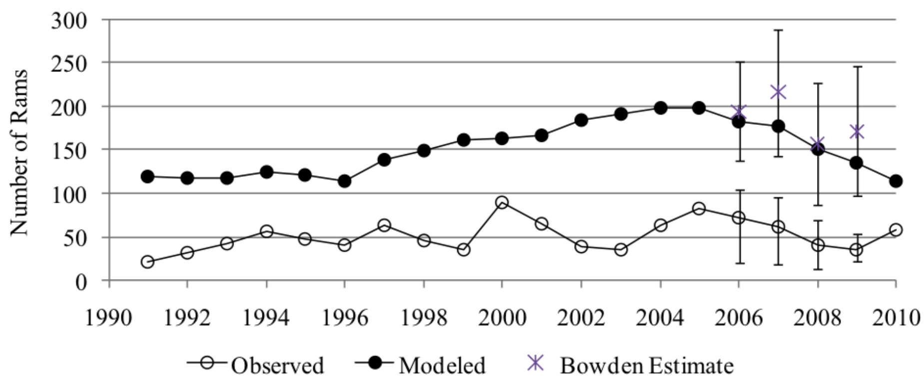

Figure 6. Number of bighhorn sheep rams observed during the July survey of the Georgetown bighorn sheep herd, Colorado, 1991-2010; the modeled ewe population for the same time period and the Bowden population estimate with 95% confidence intervals from the mark-resight study 2006-2009. For years in which multiple surveys were conducted, the mean and range of the number of bighorn observed over all the surveys is shown.

varied from survey to survey due to factors, such as bighorn distribution and activity, weather conditions, group size, and, possibly, observer bias (Bodie et al. 1995; Conroy et al. 2014). Mean sighting probabilities increased annually for Pikes Peak ewes but the same trend did not occur for Georgetown ewes. Many of the same observers were used over the course of the Pikes Peak study and likely became better at finding bighorns, especially ewes, over time. In contrast, observers in the Georgetown study tended to be either novel each year or experienced with the area and less likely to improve during the years of the study. For Pikes Peak rams, mean sighting probabilities increased between 2007 and 2008 but fell in 2009. For Georgetown rams, mean sighting probabilities declined over the course of the study.

Several previous studies have reported bighorn sighting probabilities (Table 5). McClintock and White (2007) reported ewe sighting probability on summer ground-based resight surveys in Rocky Mountain National Park of 0.39 and 0.33 for 2 years. This result falls between the sighting probabilities of the Pikes Peak and Georgetown herds. Their study area was a mix of alpine and timbered areas

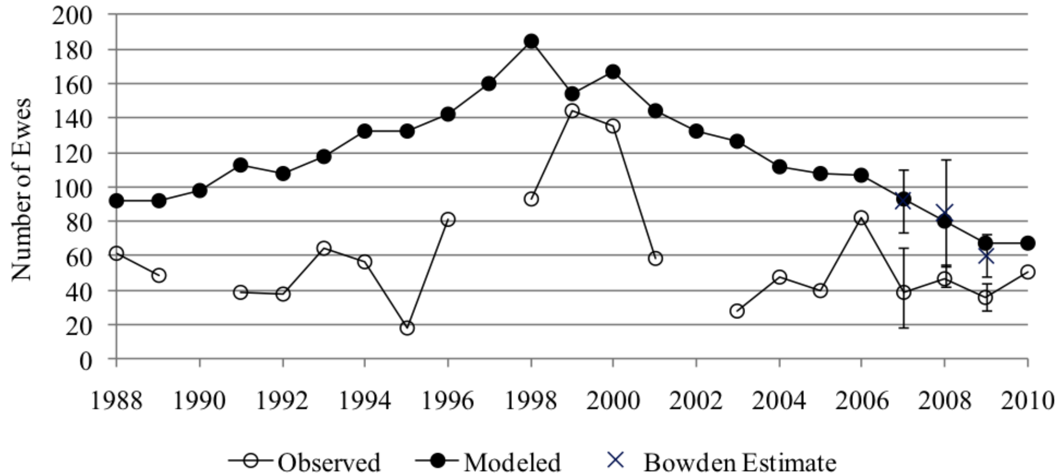

Figure 7. Number of ewes observed during the July survey of the Pikes Peak bighorn sheep herd, Colorado, 1991-2010; the modeled ewe population for the same time period and the Bowden population estimate with 95% confidence intervals from the mark-resight study 2007-2009. For years in which multiple surveys were conducted, the mean and range of the number of bighorn observed over all the surveys is shown.

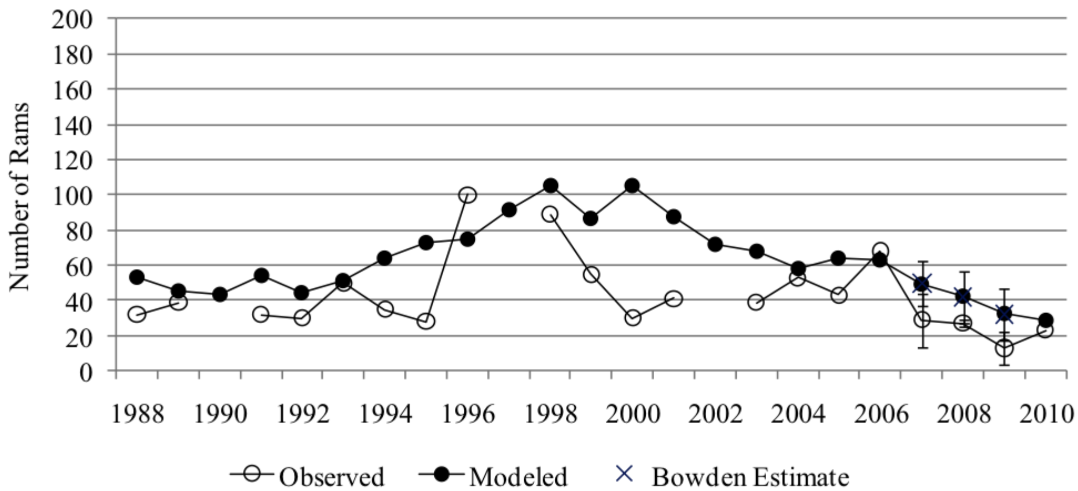

Figure 8. Number of rams observed during the July survey of the Pikes Peak bighorn sheep herd, Colorado, 1991-2010; the modeled ewe population for the same time period and the Bowden population estimate with 95% confidence intervals from the mark-resight study 2007-2009. For years in which multiple surveys were conducted, the mean and range of the number of bighorn observed over all the surveys is shown.

similar to the habitats used by the Georgetown herd excluding the lower elevations. Direct comparisons of sighting probabilities from the other studies are difficult due to differences in seasonality, resight methods, terrain and vegetation; however, comparisons relative to several factors are possible. Conroy et al. (2014) found that, during aerial surveys, the probability of detecting desert bighorn sheep groups increased as group size increased. Bodie et al. (1995) found that group size was not related to sightability during helicopter surveys. George et al. (1996) reported higher ewe sighting probability during helicopter surveys of an alpine herd (Kenosha herd - 0.95) compared to an adjacent herd occupying a timbered habitat (Tarryall herd - 0.61). George et al. (1996) also found higher variability in bighorn sighting probability in timbered habitats than in alpine habitats. Both of these

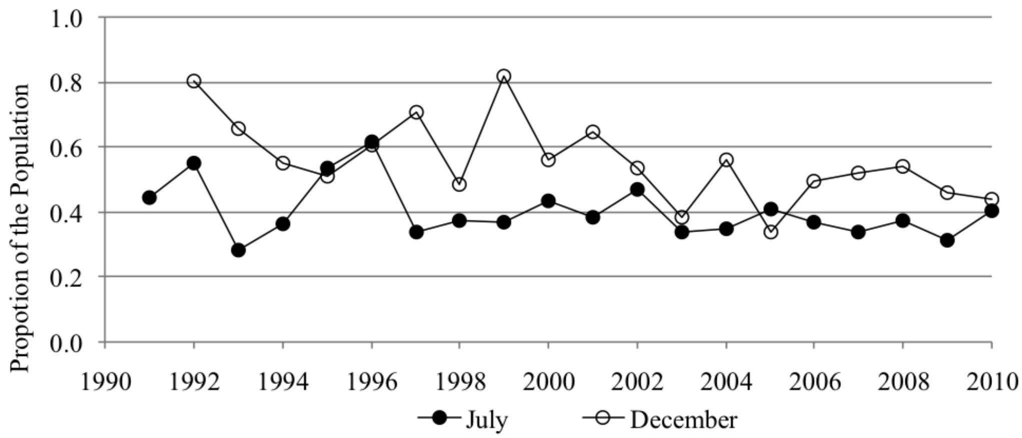

Figure 9. Proportion of modeled total population observed during the July and December surveys in the Georgetown bighorn sheep herd, Colorado, 1991-2010.

findings are consistent with our study in which the sighting probability of both ewes and rams was higher in the Pikes Peak herd than in the Georgetown herd and variability in sighting probability was higher in the Georgetown herd than in the Pikes Peak herd. George et al. (1996) reported ewe sighting probability higher than ram sighting probability in late winter helicopter surveys of alpine habitat. Bodie et al. (1995), on the other hand, reported ram sightability as higher than that of ewes in summer helicopter surveys in canyon habitat. In the current study, ewe sighting probability was higher than that of rams in the Georgetown herd; the opposite was true in the Pikes Peak herd.

Mark-resight methods proved effective for estimating the bighorn population in both herds. These estimates were more precise for the Pikes Peak herd, in which a greater proportion of the

Table 5. Mean bighorn sheep sighting probabilities reported in previous studies.

Class	Sighting probability	State	Population	Habitat	Resight method	Season	Citation
Ewe	0.61	CO	Tarryall Mt	Timbered	Helicopter	Winter	George et al. 1996
Ewe	0.95	CO	Kenosha	Alpine	Helicopter	Winter	George et al. 1996
Ewe	0.39, 0.33[a]	CO	Rocky Mountain National Park	Alpine/timbered	Ground	Summer	McClintock and White 2007
Ewe	0.24[b]	CO	Georgetown	Alpine/timbered /canyon	Ground	Summer	This Study
Ewe	0.44[c]	CO	Pikes Peak	Alpine	Ground	Summer	This Study
Ewe	0.57	ID	Little Jacks Creek	Canyon	Helicopter	Summer	Bodie et al. 1995
Ewe	0.58	CO	Trickle Mt		Helicopter	Winter	Neal et al. 1993
Ram	0.50	CO	Kenosha	Alpine	Helicopter	Winter	George et al. 1996
Ram	0.17[d]	CO	Georgetown	Alpine/timbered/ canyon	Ground	Summer	This study
Ram	0.49[e]	CO	Pikes Peak	Alpine	Ground	Summer	This study

[a]2003 and 2004 reported separately

[b,c,d,e] Many marks were not uniquely identified. The mean proportion of collars observed was [b] 0.30, [c] 0.51, [d] 0.25, [e] 0.54

herd was marked and observed during surveys compared to the Georgetown herd. Within each herd and year, demographic ratios varied widely between individual surveys (Table 6). The variability in demographic ratios can be attributed to the heterogeneity in the groups observed and missed on individual surveys. Sexual segregation during the summer counts added to variability in the sex ratio.

In the Georgetown herd, we were able to compare the proportion of the herd observed during July surveys to that of December surveys. Even though 2-3 times more routes were completed on each of the surveys in July than surveys in December, the proportion of the herd observed was higher in December. This was due to the fact that in December bighorn are concentrated on winter range that is easily accessible to survey and that ewes and rams were engaged in rutting behavior, which makes them more active and visible.

Adult survival did not appear to be limiting population growth in either herd. In the Georgetown herd, mortality resulting from collisions with vehicles was estimated at 8% of the population per year during the study (Huwer 2010, 2015). This mortality was dispersed along the interstate and major highways that pass through the range of the herd with speed limits up to 65 miles per hour. The Georgetown bighorn were vulnerable to being struck by vehicles when crossing, feeding adjacent to and licking salt from these roadways. Vehicle-caused mortalities have been recorded in every month of the year; however, most mortality occurred in April, followed by November. None of the collared bighorn in the Pikes Peak herd died as a result of being struck by a vehicle.

Even though the leading causes of adult mortality were very different between the herds, the non-harvest adult ewe and ram survival rates were similar. This raises the question of whether mortalities resulting from mountain lion predation and vehicle collisions were largely compensatory in these specific herds during the respective studies. Both the Pikes Peak and Georgetown herds were declining from peak population numbers and experiencing low lamb recruitment during these studies, possibly indicating some level of density dependent response, such as disease, may have been operating. Bronchopneumonia was known to be prevalent in both herds (Huwer 2010, 2015, Stiver 2011). In the Sheep River bighorn herd in Alberta, Ross et al.

Table 6. Means and ranges of adult ewes and adult rams, lamb:ewe, and ram:ewe observed during resight surveys in the Georgetown and Pikes Peak bighorn sheep herds, Colorado, 2006-2009.

	Bighorn Sheep Herd						
	Georgetown Herd				Pikes Peak Herd		
	2006	2007	2008	2009	2007	2008	2009
Number of surveys	6	6	5	5	7	6	6
Routes per survey	11-14	13-16	13-15	13-15	9	10-11	11
Mean observed lamb:ewe	0.27	0.43	0.36	0.40	0.50	0.45	0.24
Range of observed lamb:ewe	0.15-0.55	0.18-0.54	0.16-0.54	0.24-0.47	0.33-0.82	0.24-0.64	0.04-0.42
Mean observed ram:ewe	1.19	1.05	0.66	0.83	0.79	0.60	0.36
Range of observed ram:ewe	0.48-2.09	0.22-2.23	0.23-1.38	0.40-1.33	0.52-1.32	0.45-0.65	0.13-0.79
Mean no. of ewes observed	60	58	60	47	39	47	36
Range no. of ewes observed	33-93	40-81	50-74	36-63	19-65	42-55	28-44
Mean no. of rams observed	71	61	40	36	29	27	29
Range no. of rams observed	21-105	18-96	14-69	22-53	17-44	24-29	4-22

(1997) found that more than 30% of lion-killed bighorn sheep appeared to have disabilities prior to death. In northern Colorado, mule deer (*Odocoileus hemionus*) infected with chronic wasting disease were more likely to be killed by vehicle collisions or mountain lions than uninfected deer (Krumm et al. 2005, 2010). Bighorn with bronchopneumonia in the Pikes Peak and Georgetown herds may have been more susceptible to vehicle collisions and mountain lion predation than healthy bighorn due to reduced levels of alertness. In addition, most of the major roadways within the range of the Georgetown herd run along creeks through the low elevations of the range. Bighorn with compromised respiratory health may have been likely to spend more time in valley bottoms than on steep slopes and high elevation portions of their home range, bringing them into close proximity to major roadways. Indeed, in cases of bronchopneumonia die-offs, carcasses are frequently found along creeks in canyons and at the base of escape terrain.

MANAGEMENT IMPLICATIONS

For many bighorn populations, no studies have been conducted to estimate the population sizes with known levels of precision. Managers, in these cases, often apply an upward adjustment to minimum count data to estimate population size. The size of the upward adjustment required depends on survey methods and characteristics of the herd and its habitat. The Georgetown and Pikes Peak herds occupy areas characteristic of other bighorn habitat in Colorado. Our studies provide sighting probabilities, proportions of collars observed and proportions of modeled populations observed during ground based surveys for 2 herds that differ in size, habitat use, and survey coverage. These results can be used to inform the size of the upward adjustments applied to minimum counts obtained through ground counts in other herds.

During both the summer and fall surveys, the proportion of the herd, the sex ratio, and the age ratio observed on a specific day are variable, depending on environmental conditions and bighorn distribution on the day of the survey. For many herds in Colorado, only 1 survey is conducted per year and annual variation in the results is high. In these herds, more reliable data can be collected and conducting multiple surveys per season can reduce annual variability.

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