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COMPARISON OF MARK-RESIGHT POPULATION SIZE ESTIMATORS FOR BIGHORN SHEEP IN ALPINE AND TIMBERED HABITATS

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Abstract: We conducted mark-resight surveys using 50 radio-collared bighorn sheep (*Ovis canadensis*) distributed across three interconnected subpopulations in the Kenosha and Tarryall Mountains, Colorado. Population size of the Kenosha Mountains subunit was estimated based on data from 2 helicopter flights using both the joint hypergeometric maximum likelihood estimator (JHE) and Bowden's estimator in the program NOREMARK; population size of the Tarryall Mountains subunit was estimated based on data from 3 helicopter flights using JHE. We observed close agreement between the 2 estimators in the Kenosha Mountains: population estimates (90% confidence intervals) were 97 (87-115) using JHE and 96 (80-116) using Bowden's estimator. In the Tarryall Mountains subunit, JHE provided a population estimate of 148 (136-164). The difference in sighting probability between sexes approached significance ($P = 0.074$ and 0.013) with sighting probabilities for marked ewes (0.9 and 1.0; $n = 10$) being greater than for marked rams (0.5 on both occasions; $n = 6$). Sighting probabilities did not vary over occasions in the Kenosha Mountains subunit (0.75 and 0.81) ($P = 0.67$), but did vary in the Tarryall Mountains subunit (0.88, 0.32, 0.65) ($P < 0.0001$). We conclude that sighting probabilities for bighorn may be similar over sighting occasions in alpine and adjacent subalpine habitats, but may vary widely in timbered habitats. Because Bowden's estimator allows sighting probabilities to vary among individuals and with factors like vegetation cover, we recommend its use in analyzing mark-resight data to estimate bighorn sheep populations in timbered habitats.

Keywords: (*Ovis canadensis*), population estimation, mark-resight, sighting probabilities.

Population size estimates for bighorn sheep vary greatly in reliability (Bailey, 1990). Bighorn are normally found in steep, rugged terrain that is often associated with limited human access (Geist 1971). As a result, bighorn censuses are expensive and time consuming. In addition, bighorn sheep population estimation has not received as much attention as for deer and elk. As a result, most bighorn herd estimates have been based on impressions (Bailey, 1990), counts with no adjustments for sightability (Cook et al. 1990, Bodie et al. 1990, Karasek et al. 1992), and counts with some standard adjustment (15-33%) (Skjonsberg 1988, George unpubl. data).

Recently, methods using marked bighorn to estimate the proportion of populations that were missed on helicopter surveys have been used to estimate bighorn populations. These methods have included mark-resight surveys (Leslie and Douglas 1979, 1986, Remington and Welsh 1993, Neal et al. 1993) in desert and foothills habitats, and a sightability model (Bodie et al. 1995) for canyon habitats. Many bighorn herds in Colorado are found in mountain habitats with canopy cover where mark-resight surveys have not been applied and Bodie et al. (1995) did not recommend using their sightability model.

The bighorn herd in the Kenosha and Tarryall Mountains uses both open and timbered habitats. Historically, population estimates have been based on counts of sheep at bait sites, field persons' judgement, and intermittent summer ground counts in the Kenosha Mountains. Recently, helicopter counts have been used in the Kenosha subpopulation to obtain minimum population numbers and were adjusted upward for a population estimate of 100. During the same time period, some field persons voiced concern that population size of the Tarryall subpopulations was overestimated.

Concurrent radio-telemetry studies in the Kenosha and Tarryall Mountains provided the opportunity to conduct mark-resight inventories. Our objectives were to: 1) estimate bighorn population size using mark-resight surveys; 2) compare sighting probabilities of marked bighorn among sexes, sighting occasions and subunits; and 3) compare 2 population estimators' performance and compliance with their respective assumptions.

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STUDY AREA

The study area was located in Park County in central Colorado (39° N, 105° W). We divided it into 2 subunits which included all known and suspected ranges of 3 bighorn subpopulations. The Kenosha Mountains (KM) subunit was approximately 65 km^2 and contained 1 subpopulation that ranged in the Kenosha and Platte River Mountains, and N. Tarryall Peak area. Elevation ranged from 2,800 - 3,800 m. Bighorns were primarily found on alpine tundra and on mixed grass slopes interspersed with bristlecone pine (*Pinus aristata*), Douglas fir (*Pseudotsuga menziesii*), ponderosa pine (*Pinus ponderosa*), Englemann spruce (*Picea englemannii*) aspen (*Populus tremuloides*) and rock outcrops. Willows (*Salix* spp.) and large stands of conifers were used occasionally. Escape cover consisted of rock outcrops that seldom exceeded 100 m in vertical relief.

The Tarryall Mountains (TM) subunit, was approximately 130 km^2, abutted the southeastern boundary of the KM, and contained 2 bighorn subpopulations. Topographic relief was greater than in the KM, with cliffs and rock outcrops often exceeding 200 m in vertical relief. Elevation ranged from 2400-3800 m. During March and April most bighorn used mixed grass slopes interspersed with ponderosa pine, Douglas fir, bristle cone pine and aspen, and riparian meadows along Tarryall Creek. Bighorn also used steep, broken slopes with conifer cover approaching 50%. Alpine tundra and dense stands of Douglas fir and Englemann spruce received little use in winter and early spring.

METHODS

We captured bighorns in the TM and KM with drop-nets or by immobilization with carfentanil delivered by a dart gun. On one occasion we used helicopter net gunning to capture sheep in the TM. Capture occurred on multiple dates, during November - February 1991-95, at 3 separate sites in an effort to disperse marked sheep throughout the study area. Bighorns were aged, sexed, fitted with radiocollars and released. Each collar had a unique radio frequency in the range 148-149 MHz and, in the KM, each collar was uniquely marked for visual identification from a helicopter. Fifty marked bighorn (34 adult ewes in the TM and 10 adult ewes and 6 adult rams in the KM) were used in mark-resight surveys.

We conducted 3 helicopter resight surveys during late March and early April, 1995. This time was chosen because bighorns concentrated in open areas (alpine tundra, south-facing slopes and meadows), they were more reluctant to use timbered areas to avoid the helicopter (George and Mason, unpubl. data) and the earliest parturition dates were at least 1 month later (S. Roush, pers. commun.). Bighorn range in the entire study area was searched on the first 2 flights, but due to flight time restrictions and weather, only the TM was counted on the third flight. Surveys were separated by at least 5 days to minimize effects on bighorn sightability on following surveys and to reduce stress on the animals.

To minimize differences between surveys, the same helicopter (Bell 47 Soloy), pilot and primary observer were used on all flights. However, the secondary observer varied. When a group of bighorn was spotted, the location was noted, and the animals were followed, counted, and scrutinized for marks. In the KM, marked bighorn were individually identified. Afterward, the helicopter returned to the previous flight path. Immediately after each survey, all marked bighorn were located from the ground with telemetry receivers to confirm that they were alive and within the study area.

Population sizes in both subpopulations were estimated using the joint maximum likelihood estimator (JHE), as recommended for mountain sheep by Neal et al. (1993), using the program NOREMARK (White 1993, 1996). In addition, individually identifiable marks in the KM allowed population size estimation with the Bowden's estimator (Bowden and Kufeld, 1995) in NOREMARK. We used the Chi-square statistic to test for differences in mean sighting probabilities.

RESULTS

There was close agreement between the JHE and Bowden's estimator in the Kenosha Mountains (Tables 1 and 2). Population estimates (90% confidence intervals) were 97 (87-115) using JHE and 96 (80-116) using Bowden's estimator. The 90% confidence interval was slightly smaller for JHE than for Bowden's estimator, but both were less than $\pm$ 21%.

In the TM, the JHE provided a population estimate of 148 (136-164) (Table 3). The confidence interval was smaller ($< \pm$ 11%) than the confidence intervals for the KM's population estimates.

Sighting probabilities of marked ewes (0.9 and 1.0) were greater than sighting probabilities for marked rams (0.5 on both flights) (χ^2=3.2; df=1; P = 0.074 and χ^2=6.154; df=1; P = 0.013) in the KM (Table 4). Data was not pooled because the same bighorn were involved in both flights.

In the KM, each of the 10 marked ewes was seen at least once and 9 were seen on both flights. On 30 March, only ewe "5" was missed. On 5 April, all 10 marked ewes were seen.

Two marked rams were seen on both flights, 2 were seen on 1 flight, and 2 were not seen on either flight. On 30 March, rams "X", "F", and "P" were observed. On 5 April, rams "X", "F", and "J" were observed. Rams "H" and "K" were not observed on either flight.

The proportion of marked bighorn seen did not vary over flights in the KM (0.75 and 0.81) (P = 0.67), but did vary significantly in the TM (0.88, 0.32, 0.65) (P < 0.001) (Table 5).

DISCUSSION

Population Size Estimates

In the KM, population estimates from the JHE and Bowden's estimators (97 and 96) were close to the prior population estimate of 100. The prior estimate was obtained from helicopter counts adjusted upward approximately 20% based on "professional judgement." Skjonsberg (1988) also adjusted fall-winter helicopter counts in alpine terrain to account for a high proportion of the bighorn that were present. He used an upward adjustment of 15% to estimate population size. Sighting probabilities in the KM support the judgement that from 75-85% of bighorn are counted on helicopter counts in alpine and adjacent subalpine habitats during winter or early spring.

The population estimate for the TM provided by the JHE (148) was approximately 40% lower than the previous estimate of 250, and similar to the minimum number of sheep observed in the subunit that winter (156) (J. Vayhinger, pers. commun.). The previous estimate was based on counts at bait sites and professional judgement. The JHE mark-resight population estimate may have underestimated the TM subpopulation because only ewes were marked. If sighting probabilities for rams was lower than for ewes in the TM as we observed in the KM, the ram portion of the TM population may have been underestimated. However, it is doubtful that the ram underestimate would account for the entire 40% difference.

Sighting Probabilities

There is little published information on sighting probabilities for bighorns. Consequently, sighting probabilities observed in this study area can be compared to only 2 other studies. The mean sighting probability for marked ewes of 0.61 in the TM was similar to those observed for marked ewes by Neal et al. (1993) (0.58) and Bodie et al. (1995) (0.57). The mean sighting probability for marked ewes of 0.95 in the KM was higher than has been reported.

The sighting probabilities of ewes were greater than for rams in the KM. Bodie et al. (1995) observed the opposite relationship in Idaho with sightability for rams being greater than for ewes. These authors observed that rams were more likely to use habitats with greater visibility (flats and open slopes), whereas ewes used habitats with less visibility near escape cover (canyons). Their study area contained few trees.

We observed that rams were more likely to be near conifers and aspens than ewes which may have aided rams in avoiding detection. Rams also used a wider variety of habitats and ranged further from escape cover than ewes. Consequently, identifying search areas was less predictable for rams than for ewes. In the KM, rams were hunted, but ewes were not. Thus, rams may be more likely to use timber to avoid detection by hunters.

Weather may have affected sighting rates in the TM more than in the KM. The proportions of marked bighorn observed in the TM (0.88, 0.32, and 0.65) were significantly lower and more variable than in the KM. The best conditions occurred on 30 March and corresponded to the highest sighting rate in the TM. There was 100% snow cover that was less than 24 hours old during most of the survey, light winds, and partly cloudy skies. The poorest conditions occurred on 5 April; the same date as the lowest sighting rate in the TM. Snow cover was less than 50% with winds gusting to 50 kph, and flat light.

Other factors may have contributed to the variability among and within subunits. In the KM, we had predetermined the most effective flight plan for counting bighorn from 5 previous helicopter bighorn counts

Table 1. Mark-resight population estimate statistics from helicopter counts of bighorn sheep in the Kenosha Mountains, Colorado, 1995.

Date	No. Marked	No. Marked Observed	No. No. Unmarked Observed	Lincoln-Petersen Estimate
30 Mar	16	12	63	98.4
5 Apr	16	13	64	93.7
Pop. estimate (90% CI)				97 (87 - 115)

Table 2. Mark-resight population estimate statistics for Bowden's estimator from helicopter counts of bighorn sheep in the Kenosha Mountains, Colorado, 1995.

No. marked	16	
No. unmarked observed	127	
No. marked observed	25	(2 sheep observed 0 times, 3 sheep observed 1 time, 11 sheep observed 2 times.)
Population estimate (90% CI) 96	(80 - 116)	

Table 3. Mark-resight population estimate statistics from helicopter counts of bighorn sheep in the Tarryall Mountains, Colorado, 1995.

Date	No. Marked	No. Marked Observed	No. No. Unmarked Observed	Lincoln-Petersen Estimate
30 Mar	34	30	90	135.6
5 Apr	34	11	44	162.3
12 Apr	34	22	85	163.3
Pop. estimate (90% CI)			148 (136 - 164)	

Table 4. Sighting probabilities of marked bighorn rams and ewes in the Kenosha Mountains, Colorado, 1995. *P* value is a test of equal sighting probabilities of rams and ewes.

Date	No. Marked		No. MarkedObserved		SightingProbability		*P*
	Ram	Ewe	Ram	Ewe	Ram	Ewe	
30 Mar	6	10	3	9	0.5	0.9	0.074
5 Apr	6	10	3	10	0.5	1.0	0.013

Table 5. Sighting probabilities of marked bighorn sheep in the Kenosha and Tarryall Mountains, Colorado, 1995. *P* values are a test of equal sighting probabilities across sighting occasions.

Location/Date	No.Marked	No. MarkedObserved	SightingProbability	*P*
Kenosha Mountains				
30 Mar	16	12	0.75	
5 Apr	16	13	0.81	0.67
Tarryall Mountains				
30 Mar	34	30	0.88	
5 Apr	34	11	0.32	<0.0001
12 Apr	34	22	0.65	

during the 2 preceding years. However, in the TM, complete helicopter counts had not occurred prior to this study, so a firm flight plan had not been established. Observer bias may have contributed considering that the secondary observer changed between flights and the primary observer was more familiar with the KM study area.

Estimator Comparison

We observed close agreement between population estimates provided by the JHE and Bowden's estimators in the KM. They varied by approximately 1% and were larger than the minimum number of sheep known to be in the subpopulation. Bowden's 90% confidence interval was 28% larger than, but overlapped and included, the JHE's.

Both estimators have requirements and assumptions that must be met to estimate population numbers without bias and with good precision. The JHE estimator is based on the Lincoln-Petersen estimator which requires that: 1) the population is closed geographically and demographically; 2) animals must not lose marks; 3) all marked animals are correctly identified, counted and recorded and 4) all animals (marked and unmarked) must have the same, independent probability of being sighted during individual sighting occasions (Otis et al. 1978).

We believe that the first 3 assumptions of the JHE estimator were completely met, but the fourth was not. Relocations of marked bighorn after each flight confirmed that all remained in the study area and no marks were lost. We believe that all marked bighorn were correctly identified, counted and recorded. However, the difference in sighting probabilities between sexes and subunits indicate that all animals did not have the same probability of being sighted. Neal et al. (1993) and White (1993) found that estimated confidence coverage for the JHE was too small if sighting probabilities varied, but estimates were relatively unbiased.

Marked animals should be representative of the population. We captured bighorns in the KM during the breeding season to minimize differences in capture probabilities between sexes. Although 1 bait site was used, we dropped the net on 2 different groups of bighorn and darted on a third occasion. Observations indicated that marked sheep dispersed throughout the KM and few groups were observed without at least 1 marked sheep. However, we avoided placing radiocollars on lambs and yearling rams, so the assumption of a representative sample was not met completely. We believe that sighting probabilities for lambs and yearling rams were similar to the ewes that they associated with.

Unlike the JHE, Bowden's estimator allows sighting probabilities to vary among individuals and can depend on such factors as group size and vegetation cover (Bowden and Kufeld 1995). It is easy to calculate and does not require independent population sighting trials or even separate population sighting trials. The procedure does require: 1) animals must be marked so they are individually identifiable; 2) the number of times each marked animal is sighted is recorded without error; 3) the number of unmarked animals is recorded without error; 4) the sighting process is independent of the mark status of the animal; and 5) animals are selected for marking in a manner equivalent to selecting a simple random sample.

The first 4 requirements of the Bowden's estimator were met in the KM, but the fifth was not completely met. Animals were individually identifiable and we believe that marks did not affect sighting probabilities. As described above, we attempted to obtain a random sample within logistical constraints, but the requirement of equal capture probabilities was not met completely. The effect on population estimates and associated confidence intervals is unknown, because the bias from this violation is a function of how nonrepresentative the sample is of the population.

CONCLUSIONS

Sighting probabilities for bighorn on helicopter census may be similar over sighting occasions in alpine and adjacent habitats, but may vary widely in timbered habitats. Sighting probabilities also varied between sexes.

The reliability of bighorn population estimates can be improved by using marked animals in mark-resight inventories and by measuring sighting probabilities. Bowden's estimator is recommended over the JHE estimator because it allows sighting probabilities to vary among individuals. Although complete compliance with assumptions is difficult, mark-resight estimates and associated sighting probabilities allow managers to base population estimates on rigorously estimated parameters rather than judgement alone. Although professional judgement is often supported by observed data, rigorously estimated values are more defendable and reliable, with their confidence intervals providing measures of precision.

We recommend that managers take advantage of situations where bighorn populations will be studied using radio-telemetry collars and plan to include mark-resight population surveys. It is inexpensive to attach individually identifiable marks to radiocollars. The only additional expense will be for helicopter and personnel time to conduct resight surveys.

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