Mark–resight density estimation for American black bears in Hoopa, California

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Abstract: Accurate and precise population estimates are necessary to answer many management questions, but these estimates are generally unavailable for large carnivores because of their extensive movements, low densities, and secretive natures. These traits also often prevent the bounding of occupied areas necessary to estimate densities. We used a modified Petersen mark–recapture methodology to estimate black bear density in 1998 at 2 study sites on the Hoopa Valley Reservation, California, from mark–resight data. We used culvert traps to capture, radiocollar, and eartag bears, radio telemetry to establish closure, and remote cameras to collect resighting data. We calculated bear densities (90% confidence intervals) of 0.18 (0.09–0.32) and 1.33 (0.54–3.29) bears/km2 on the 2 sites. Knowledge of bear densities can now be incorporated into forest management actions and associated bear control measures on the Hoopa Valley Reservation.

Key words: American black bear, density, Hoopa Valley Reservation, mark–recapture, mark–resight, Northern California, Ursus americanus

American black bear damage to pre-harvest timber has been identified as a threat to the economy of the Hoopa Valley Tribe in northwestern California. Black bear (Ursus americanus) damage on the Hoopa Valley Reservation was projected to cause >$364,000,000 of losses on 17,806 ha of managed timberland from 1995 to 2045 (Abbott 1994). In response, the Hoopa Valley Tribal Forestry Department considered lethal control measures of black bears to reduce the amount of foraging damage on timber-managed Douglas-fir (Pseudotsuga menziesii) trees. Thus, it was important for reservation land managers to quantify bear density to assess the consequences of lethal control measures and develop appropriate management strategies for minimizing damage to commercial timberland.

Accurate population estimates for large carnivores are generally unavailable because of these species’ extensive movements, low densities, and secretive natures. Few actual density estimation techniques have been successfully applied to large carnivores because the logistics of capture and the expense and difficulty of recapture; resulting sample sizes are often too small and variable to effectively drive population models.

Miller et al. (1987) developed a method for estimating density using fixed-wing aircraft to collect resighting data and establish closure of the study area. However, Miller et al. (1987) and Garshelis (1992) reported the method was feasible only in open habitats where animals can be readily resighted. Because over 95% of the Hoopa Valley Reservation is composed of forested habitat, we could not estimate bear population by applying the Miller et al. (1987) method. Garshelis (1992) presented a technique based on a method by Kenward et al. (1981) to estimate density of bears in forested habitats. However, this technique did not allow for estimation of variance because the number of points used to correct for violations of geographic closure could not be incorporated into the variance equation presented by Kenward et al. (1981). Bowman et al. (1996) developed a mark–resight estimation technique, but were unable to determine the number of marked animals on their study area and failed to achieve geographic closure necessary to estimate density. Grogan and Lindzey (1999) established geographic closure by multiplying a weighted-mean density estimate by the average amount of time marked bears occupied their study area during the resighting sessions; thus, they were able to use
marking and resighting to estimate density. More precise density estimates would be available by determining the amount of time each marked animal occupied the study area, rather than using an average of the amount of time marked animals occupied the study area in calculating population density. This idea was incorporated into our density-estimation model.

The Petersen estimate of population size, for 2 sample occasions, is calculated as the total number of animals resighted in the second sample divided by the proportion of marked animals recaptured or resighted in the second sample (Nichols et al. 1981, Seber 1982, White et al. 1982, Minta and Mangel 1989, Bowden and Kufeld 1995). Bowden (1993) and Bowden and Kufeld (1995) presented a general statistical model for mark–sight experiments and analytical methods of constructing confidence intervals on a modified Petersen estimator applied to mark–resight data (White 1996). The Bowden model is an approximately unbiased estimator, with confidence intervals computed from the variance of the sighting frequencies of the marked animals (Bowden 1993, White 1996).

To convert a mark–resight estimate of abundance (Bowden 1993, Bowden and Kufeld 1995) to an estimate of density requires defining the bounded area of sampling. Several approaches using radiotelemetry techniques have been used to establish geographic closure for populations of large carnivores (Miller et al. 1987, McLellan 1989, Garshelis 1992, Grogan and Lindzey 1999, Soisalo and Cavalcanti 2006). Garshelis (1992) calculated animal-equivalents for each radiocollared individual according to the proportion of time it spent on the study area. This addressed the bias that could result when animals with large home ranges routinely cross study area boundaries, and avoided the assumption that all animals were full-time residents of the study area (White et al. 1982, Miller et al. 1987, McLellan 1989, Garshelis 1992). Our objective was to describe application of the concept of animal-equivalents (Miller et al. 1987, McLellan 1989, Garshelis 1992) to the Bowden model (Bowden 1993, Bowden and Kufeld 1995) to estimate population size with a measure of variance for black bear on the heavily-forested Hoopa Valley Reservation.

Study area

The Hoopa Valley Reservation (Fig. 1) is located in the Klamath Mountains of northern California. The area of the reservation is approximately 356 km², and elevation levels range between 98 and 1170 m. Approximately 339 km² of the reservation are forested, with Douglas-fir, tanoak (Lithocarpus densiflorus), and madrone (Arbutus menziesii). Other species include Oregon white oak (Quercus garryana) and California black oak (Q. kelloggii). The shrub layer was generally dominated by evergreen huckleberry (Vaccinium ovatum), tobacco brush (Ceanothus velutinus), or salal (Gaultheria shallon). The non-forested areas were made up of urban areas, natural prairies, large rock outcrops, and brush fields, which were irregularly distributed through the otherwise forested landscape.

Logging of old growth Douglas-fir on the reservation began in the mid 1940s and became intensive in the late 1950s. By 1994, intensive logging reduced the extent of mature and old growth forest to approximately 49% of historic levels. In 1998 the Reservation contained approximately 305 km² of commercial timberland with about 1.2 billion board feet of commercially important timber species.

We selected two 5-km² study sites separated by approximately 4 km and the Trinity River, within the forested northern portion of the reservation (Fig. 1). Study site selection was constrained by size of the reservation, a 19 x 19 km square, and our interest in selecting areas with different levels of bear-related tree damage but similar habitat characteristics. These sites had approximately equal elevation ranges, elevation of center points, meters of roads, meters of creeks, and areas of similarly managed timber stand types and ages.

Methods

We selected 10 trap locations in each study site based on road availability and access, potential of the trap being seen by the general public, terrain suitability for bear immobilization, and effective coverage of the study sites. We used 2 culvert traps (94 cm diameter x 183 cm long) baited with fish in each area. Traps remained at each trap location for 8–10 nights and were visibly examined at approximately 0800 and 1600 daily between 6 July and 24 September 1998.

We immobilized captured bears using tiletamine/zolazepam with a jab stick delivery system administered at 2.9–6.8 mg/kg depending on the bear and capture conditions (Burton and Schmalenberger 1995). On some bears we used 2 mg/kg of ketamine.
hydrochloride and 1 mg/kg xylazine hydrochloride (Schroeder 1986).

Captured bears were radiocollared (Model 500, Telonics, Mesa, Arizona, USA) and tagged in each ear with colored and uniquely numbered Fearing Small Round Hog Litter Tags (Fearing Corporation, South St. Paul, Minnesota, USA). Each captured bear was photographed to aid in resighting identification.

**Resighting period**

The resighting period was 28 September to 5 November 1998. We used photographs from cameras at 8 locations on each site to record resightings of marked and unmarked bears during the 38-day resighting period. The camera stations consisted of 119 cm lengths of 38.7 cm diameter PVC culvert pipe with a converted 35 mm camera (Olympus Infinity Mini DLX, Melville, New York, USA) triggered by an infrared door alarm (Radio Shack Mini PIR Alarm Catalog Number 49-425, Fort Worth, Texas, USA). This design maximized the likelihood of obtaining a head and ear photograph of each bear for more reliable identifications of marked and unmarked bears. The location for each station within the site was selected using a geographic information system (Fig. 2). Camera stations were
baited with chicken rather than fish. We changed the attractant to meet the assumption of equal sightability of marked and unmarked animals during the resighting effort (Minta and Mangel 1989). The bait and film were examined at each camera station every other day. Photographs of the same individual taken at the same camera station needed to be separated by \( >24 \) hours to be considered independent resightings. However, the same individual could have been resighted at \( \geq 2 \) camera stations within 24 hours, and these were considered independent resightings (Mace et al. 1994).

We determined the presence or absence (diurnal) of each marked bear via radiotelemetry every other day during the resighting period. Exact locations of marked bears were not generally necessary, thus radio signals were used only to determine whether a marked bear was in or out of the study site. We obtained precise locations using triangulation and visual observations when a marked bear was near a study site boundary (Miller et al. 1987, McLellan 1989, Garshelis 1992). These determinations were facilitated by high densities of roads on both sites (2.6 \( \text{km/km}^2 \)).

Fig. 2. The 8 camera station locations on the west study site of the Hoopa Valley Reservation, California, 28 Sep–5 Nov 1998. The 8 lines originated in the center of the 5-km\(^2\) area and terminated at the outer edge, at 45° intervals starting at 0°. The lines were rotated at a random rotation angle between 1 and 360°. In this case, the rotation angle was 22° clockwise. A camera station was placed at the location where each line crossed a road within the 5-km\(^2\) area. If a line did not cross a road, the station was placed on the road nearest the line within the study site. Locations selected for the camera stations were moved from the GIS (geographic information system) assignment as much as 100 m to place each station on level ground out of view of the public.
allowing us to make determinations of bear presence throughout and along the borders of each study site.

**Density estimator**
We weighted each marked bear by the proportion of time it spent on the study site during the entire resighting period (Miller et al. 1987, McLellan 1989, Garshelis 1992). This individual weighting adjusted for differing probabilities of resighting related to differing nights of camera exposure and a lack of geographic closure caused by movements across study area boundaries.

We calculated separate density estimates for the 2 study sites. A finite population of \( N \), consisting of the \( M \) marked and the remaining \( N-M \) unmarked animals alive in the study site at the beginning of the resighting period were defined in the density estimation model. The population was assumed to be demographically closed but geographically open over the 5-week resighting effort. Thus, some animals could have been off the study area occasionally and hence have a zero resighting probability (White 1996).

The Bowden model (with parameters expressed in notation presented by White 1996) and in terms of animal-equivalents (indicated by *) was used to calculate density (Bowden 1993, Bowden and Kufeld 1995, White 1996; see Appendix for empirical example of calculations):

\[
\hat{N} = \frac{u\ast + m\ast}{\bar{f}\ast + s_f^2} \left( 1 + \frac{s_f^2}{\bar{T}\ast f^2} \right)
\]

where

- \( u\ast \) was the number of observations of unmarked animals \( (u) \) multiplied by the mean animal equivalent for the study area to correct for proportional use of the study area,
- \( m\ast \) was the number of resightings of a marked animal multiplied by its individual animal equivalent, summed across all marked animals, \( \bar{f}\ast = \frac{m\ast}{T\ast} \) was the mean number of times marked animals were resighted,
- \( T\ast \) was the sum of animal equivalents in the population at the time of the resighting period, and
- \( s_f^2 \) was the variance of the resighting frequencies, calculated by:

\[
s_f^2 = \frac{\sum_{i=1}^{T} (f_i\ast - \bar{T}\ast)^2}{\bar{T}\ast}
\]

where

- \( f_i\ast \) was the number of times the \( i \)th marked animal was observed during the resighting period multiplied by its animal equivalent.

We used natural logarithm transformations of the estimators to generate 90% confidence intervals of the density estimate (McDonald and Palanacki 1989, Bowden 1993, White 1996). However, consistent with the methods of density estimation presented by Kenward et al. (1981) and Garshelis (1992), our estimate of variance did not account for the number of points used to determine animal equivalents, thus our confidence intervals were biased low. We also generated population estimates for each study site using the unmodified Bowden estimator using program NOREMARK for comparison (Bowden 1993, Bowden and Kufeld 1995, White 1996).

**Results**
We radiocollared and eartagged 7 and 8 bears on the west and east study sites, respectively. Cameras yielded 1,562 photographs during the resighting period. Of these photographs from the east site, 109 were of bears, comprising 19 independent resightings (5 marked, 14 unmarked). On the west site we had 255 photographs of bears, comprising 45 (17 marked, 28 unmarked) independent resightings. During the resighting effort, 3 and 9 resightings of bears on the east and west sites, respectively, could not be determined as marked or unmarked and were excluded from the analyses.

Five of the 8 marked bears on the east site and 6 of the 7 marked bears on the west site were relocated in the study site at least once during the 15 attempts to relocate bears using radiotelemetry and were assigned animal equivalents. We calculated density estimates and 90% confidence intervals of 0.18 (0.09–0.32) bears/km\(^2\) on the east site (Appendix) and 1.33 (0.54–3.29) bears/km\(^2\) on the west site (Table 1). Estimates of abundance and 90% confidence intervals using the unmodified Bowden estimator in program NOREMARK were 3.2 (1.8–
6.0) on the east site and 5.4 (3.2–9.4) bears/km² on the west site.

Discussion

Estimates of black bear density in North America have ranged from 0.06 bears/km² in Arizona (LeCount 1987) to 0.99 bears/km² in New Jersey (Carr et al. 2005). The magnitude of our estimates on the Hoopa Valley Reservation was consistent with several independent indicators of bear density. Capture efforts conducted between May 2001 and September 2003 across the reservation resulted in the capture of 322 individual bears on an area of 356 km² (Higley, unpublished data). Additionally, Higley (unpublished data) identified 129 bears on 26.9 km² surrounding the west study site and 46 bears on 26.6 km² surrounding the east study site. Both in the current study and subsequent efforts, no individual bear was observed on both study sites despite their proximity (4 km distant).

The high densities of bears on the reservation compared to estimates from other studies could be related to the effects of timber management on habitat and food-resource availability. Bears have been found to use managed habitats more than expected and non-managed habitats less than expected (Young and Beecham 1986, Costello 1992). Costello (1992) reported a greater availability of several seasonal food sources in managed compared to unmanaged habitats. With 305 km² of the Reservation’s 339 km² land in timber production, habitat and food availability changes could be responsible for the comparatively higher bear densities we estimated on the reservation. Additionally, hard mast has been documented as an important component in the diet and demographics of bear populations in North America (Costello 1992, Mattson 1992). The importance of tanoak mast in the diet of bears on the Reservation was indicated by the finding that 33% of bear scat collected on the reservation between April and October 1999 contained acorn (Hoopa Valley Tribal Forestry, Hoopa, California, USA, unpublished data). Hard mast and other food source variations were present around and between the 2 study sites during the capture and resighting periods. As a result, our estimates are not necessarily representative of time frames beyond the study. Reservation managers should conduct population studies to quantify the effects of management actions during the same period as the current study for comparable results.

We had anticipated that there would be a significant difference in the density of bears between the 2 sites. Both our density estimates may have been influenced by seasonal food-resource utilization by bears. Although efforts were made to select 2 similar areas, we did not account for the distribution of grasses (spring forage) or Himalayan black berries (Rubus discolor, forage available in late summer to early fall) on the 2 sites. Anecdotally, we found there to be more grasses and Himalayan black berries on and surrounding the west site than the east site. The greater abundances of these food sources and the timing of our resighting period overlapping with bear seasonal use of Himalayan black berries could have accounted in part for the remarkably large density of bears on the west site. We found that bears on the west site tended to be located in the study site more frequently (thus resulting in larger animal equivalents) than bears on

Table 1. Resighting frequencies for 7 radiocollared black bears captured on the 5-km² west site used in a mark–resight density estimate on the Hoopa Valley Reservation, California from 28 Sep to 5 Nov 1998. Animal equivalent (AE) values were calculated by dividing the number of observations of an animal in the study area by the number of total observations using radiotelemetry. Resightings were the number of independent visits to a camera station by a bear during the resighting period. The resighting frequencies (fᵢ*) were calculated by multiplying the AE values and the number of resightings. Twenty-eight unmarked observations were recorded during the resighting effort.

<table>
<thead>
<tr>
<th>Animal ID</th>
<th>Observations in study area</th>
<th>Total observations</th>
<th>Animal equivalent (AE)</th>
<th>Resightings</th>
<th>Sighting frequency (fᵢ*)</th>
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</thead>
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<tr>
<td>58</td>
<td>6</td>
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<td>1</td>
<td>0.400</td>
</tr>
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<td>15</td>
<td>0.733</td>
<td>11</td>
<td>8.067</td>
</tr>
<tr>
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<td>15</td>
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<td>0</td>
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</tr>
<tr>
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<td>0.333</td>
<td>0</td>
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</tr>
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<td>0.000</td>
</tr>
<tr>
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<td>14</td>
<td>15</td>
<td>0.933</td>
<td>1</td>
<td>0.933</td>
</tr>
</tbody>
</table>
the east site. We suspect this was a function of marked bears residing on or near patches of Himalayan black berries, which were more abundant in the west site during the resighting period. Alternatively, on the east site, berry patches were more abundant outside the site, possibly drawing marked bears out of the site during the resighting period.

Our comparatively small study sites (5 km²) and small samples, both the number of telemetry locations used to calculate animal equivalents and the number of resightings of marked animals (a function of the duration of the resighting period) probably compromised the precision of our population estimate. Increasing our study area size may have increased the precision of our estimate by decreasing edge effect (White et al. 1982). However, an increase in study area size would have resulted in the need to radiocollar additional animals (cost prohibitive in our study) or led to a larger proportion of the sample population unmarked (an alternate source of precision loss).

Garshelis (1992) noted that although proportion of time on the study area is the most justifiable weighting factor for calculating animal equivalents, there are challenges to estimating time using sample locations. Garshelis (1992) obtained weekly locations on each bear during his 8-week recapture period to calculate animal equivalents. Effort expended in more accurately assessing animal equivalents (e.g., using global positioning system collars) and increasing the number of resightings would have improved the precision of our population estimate. We were not able to incorporate the variance associated with our estimates of time spent on each study site into the animal equivalent calculation, and thus our confidence limits were biased low; however, we believe that our effort was a significant improvement over the uncorrected density estimates. Regarding the point estimates, we agree with Garshelis (1992), that the reduction in bias is worth the loss in precision and we would encourage the development of a method to estimate a true variance for this model.

The proportion of marked animals in the population being estimated is typically assumed to be the critical factor determining the repeatability and precision of a mark–recapture estimator (Caughley 1977). Based on repeated simulations, Arnason et al. (1991) argued that the precision of an estimate derived from sighting data was also affected by the number of sightings relative to the actual population size, especially for small populations with small marked fractions. Thus, the resighting period must be long enough to accurately determine the proportion of time each marked animal spent in the sampling area. We assumed marked and unmarked animals used the study sites to similar degrees. This assumption could have biased population estimates high if unmarked animals lived at the edge of the study area or were transients through it (Garshelis 1992) and were not truly part of the population on a site. Increasing the marked proportion of the population would reduce this potential bias.

The failure to correct for the proportion of time each radiocollared individual spent on the study area would have resulted in significantly inflated population estimates. The uncorrected density estimate was 17.8 times greater on the east site and 4.1 times greater on the west site than the estimates generated using our modified Bowden method. Our results indicated that the bear population on the Hoopa Valley Reservation was high compared to other areas. Tribal managers can use our results to model potential bear population control strategies, assess the effort needed to reach particular goals, and estimate the likelihood of success of achieving those goals.

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Literature cited
State University, Technical Report 93/12, Fort Collins, Colorado, USA.


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Appendix

This appendix presents an empirical example of calculating density and variance estimates using animal equivalents (AE) to the Bowden model for black bear on the 5-km² east study site on the Hoopa Valley Reservation, California from 28 September to 5 November 1998. The bears below were captured, ear-tagged, and radiocollared between 6 July and 24 September 1998, and are referred to in the model as T.

Animal equivalents were calculated by dividing the number of observations of an animal in the study area by the number of observation attempts using radiotelemetry.

Sighting frequencies (f*i) = AE multiplied by number of resightings

Unmarked observations = 14
\( u.* = \text{mean animal equivalent multiplied by unmarked observations} = 0.095 \times 14 = 1.328 \)

\[
m.* = \frac{\sum_{i=1}^{T} f_i^*}{T.*} = 0.696
\]

\[
T.* = \sum_{i=1}^{T} \text{AE} = 0.759
\]

\[
f^* = \frac{m.*}{T.*} = 0.918
\]

\[
s_{f^*}^2 = \frac{\sum_{i=1}^{T} (f^*_i - f^*)^2}{T.*} = 7.418
\]

\[
\hat{N}^* = \frac{u. + m.* + s_{f^*}^2}{f^* + f_{f^*}^2} = 0.873
\]

\[
\hat{N}^* \times \exp\left(\frac{1}{2} CV^*(\frac{\hat{N}^*}{\hat{N}^*})\right) = 1.621
\]

\[
\hat{N}^* / \exp\left(\frac{1}{2} CV^*(\frac{\hat{N}^*}{\hat{N}^*})\right) = 0.471
\]

\[
\hat{N}^* = \frac{1}{\sqrt{\text{Var}(\hat{N}^*)}} = \frac{1}{\sqrt{0.007}} = 0.980
\]

\[
CV^*(\hat{N}^*) = \frac{\text{Var}(\hat{N}^*)}{\hat{N}^*} = 0.098
\]

Confidence intervals (90% calculated here) are computed from a log-transformation as

\[
\hat{N}^* / \exp\left(\frac{1}{2} CV^*(\frac{\hat{N}^*}{\hat{N}^*})\right) = 0.471
\]

\[
\hat{N}^* \times \exp\left(\frac{1}{2} CV^*(\frac{\hat{N}^*}{\hat{N}^*})\right) = 1.621
\]