California Fish and Game 100(3):527-537; 2014

Enumerating mountain lions: a comparison of two indices

Becky M. Pierce* and Vernon C. Bleich

Sierra Nevada Bighorn Sheep Recovery Program, California Department of Fish and Wildlife, 407 W. Line St., Bishop, CA 93514, USA (BMP, VCB)

Present address: Department of Biological Sciences, Idaho State University, Pocatello, ID 83209, USA (VCB)

**Correspondent: Becky.Pierce@wildlife.ca.gov*

Assessing mountain lion (*Puma concolor*) populations is difficult due to their inherently low densities, secretive nature, and a near absence of demographically closed populations. We developed and compared two methods of indexing the number of mountain lions within a subset (referred to in this paper as the core area) of a total study area. The study area was defined as the outer boundary of combined home range polygons for all collared mountain lions. Therefore, the study area was regularly occupied by uncollared individuals whose home ranges overlapped the study area boundary. We determined through intensive capture efforts and monitoring that the much smaller core area was used only by adult mountain lions that we had identified and collared and was not used in any significant manner by uncollared adults. We derived two indices to the number of lions using the core area. One index is based on location data from VHF aerial telemetry ("fixed wing index"); the second index is based on a combination of fixed wing locations and GPS collar data combined ("location data index"). The fixed wing index yields the mean number (and variance) of adult individuals located in the core region of the study area each of 15 winters during weekly telemetry flights. The location data index is based on the sum of the proportions of locations for each individual that are within the core area each winter. The two indices were highly correlated, and the trends generally were in the same direction and changes in each were of a similar magnitude. These methods are preferable to attempting total counts because the periphery of any study area will occasionally be occupied by unmarked animals. Our methods account for those individuals, but they are not afforded the same weight as mountain lions that use the area frequently or exclusively. Managers with GPS radio collar data are encouraged to delineate a core area, where all lions known to use the area are collared, and use the sum of the proportion of locations from each individual in that area to index density, population size, number of animals present, or use.

Key words: abundance, density, index, mountain lion, puma, *Puma concolor*

There are a number of methods for assessing mountain lion (*Puma concolor*) population size and population trends; however, none of these has proven to be consistent and reliable (Jenks 2011). Further, the use of differing methods by managers among jurisdictions makes comparisons across regions difficult and questionable. Population estimators are inherently biased because the methods used to collect the data are biased. Nevertheless, many researchers believe that the most reliable estimates of density (individuals/unit area) are derived from long-term radio-telemetry studies that attempt to mark and keep track of all animals in a given geographic area (Jenks 2011). This method, however, is best considered a minimum count for which no variance can be calculated. Despite this potential shortcoming, that method is used widely by researchers and is considered the "gold standard" for determining mountain lion numbers, against which indices to mountain lion abundance should be compared (Seidensticker et al. 1973, Hemker et al. 1984, Logan and Sweanor 2001). Other methods, including non-invasive camera traps (e.g., Hughson et al. 2010), scent stations (e.g., Long et al. 2003)—or a combination of the two (Munoz-Pedreros et al. 1995)—and genetic techniques using material obtained from hair snares or feces (e.g., Ernest et al. 2000) also are problematic (see Rinehart et al. 2014 for a comprehensive review).

An index is a number that is monotonically related to population size. The best indices are linearly related to the true size of the population (Cougar Management Guidelines Working Group 2005). However, unless detection probabilities are known or estimated from the data, index values can reveal little about other parameters of interest, such as adult survival or fecundity (Anderson 2001, 2003), as re-emphasized by B. L. Pierce et al. (2012). Many indices to the abundance of mountain lions have been developed and, despite the admonition of Anderson (2003), the application of an index does not automatically imply an inappropriate procedure (Engeman 2003), as they can be useful in detecting large changes in a population or determining directional trends. Most indices, however, are never calibrated with a population of known size (B. L. Pierce et al. 2012).

Track surveys, which have been widely used for many decades are not reliable (Grigione et al. 1999) because they can be biased by habitat type, substrate, skill of the tracker, weather conditions, the likelihood of missing a transient animal, traffic volume, or the ability to distinguish among individuals. McBride et al. (2008) developed an index based on the minimum number of lions known to be alive, but it is most useful for small closed populations studied for a long period of time, such as those isolated by urbanization. However, it should not be relied upon for inferences about population trends (Cougar Management Guidelines Working Group 2005). Additionally, hunter returns can be affected by hunting effort, harvest bias for sex or age class, and variance in the ability of individual mountain lions to elude hunters.

Choate et al. (2006) reviewed the most commonly used population indices for mountain lions while testing their accuracy with radio collared populations. They found that track surveys, catch per unit effort, and other methods—such as harvest models and scent stations—performed poorly. Those authors noted, however, that multiple indices used after an initial population estimate could be used conservatively to support short-term management decisions. As a result, Choate et al. (2006) maintained that an intensive effort to radio collar individual lions is the most reliable method to enumerate population size, estimate density, and determine trends in population growth. Similarly, Rinehart et al. (2014) described biases associated with various methods of calculating population densities of secretive carnivores and concluded, "... radio-telemetry remains the most viable option for certain carnivore species, pumas among them."

Choate et al. (2006) calculated density by dividing the total number of individuals estimated to be present by the size of the study area, expressing density as the number of animals/unit area. Density estimates for species with overlapping home ranges, however, can be subject either to extrapolation bias or residency bias (Rinehart et al. 2014). Extrapolation bias results when scaling a density to a spatial extent that differs from that of the study area upon which the estimate was based; residency bias occurs when the reference area for the density estimate is inappropriate (Rinehart et al. 2014). Using a series of modeling exercises, Rinehart et al. (2014) concluded that density estimates are biased upward for open populations; estimates projected "backwards" from large to smaller areas resulted in negative bias, and the extrapolation "forwards" from a small area to a larger one resulted in positive bias.

Some genetic substructuring has been reported among mountain lion populations (Walker et al. 2001, Ernest et al. 2003), but populations in the western United States and throughout their range are rarely isolated from each other (Sinclair et al. 2001, Stoner et al. 2006, Andreasen et al. 2012). Indeed, mountain lions are capable of seasonal, long-distance migratory movements (Pierce et al. 1999), and are known to travel hundreds of kilometers when dispersing from natal areas (Thompson and Jenks 2010). Moreover, both home range size and the distribution of mountain lions can be affected by sex, or availability of resources such as prey (Seidensticker et al. 1973, Pierce et al. 2000b; see Pierce and Bleich 2003 for a comprehensive review). Therefore, the designation of a study area, based on the extent of the movements of collared mountain lions is problematic and the estimation of population size and population trends for mountain lions based on study area boundaries can be misleading.

As a result of these demographic and life history characteristics, use of a study area by known individuals whose home ranges overlap the pre-established boundaries are overestimated because some individuals might be present in the study area only infrequently. Additionally, transient animals could be counted as unique individuals, even if only present on the study area temporarily. Mountain lion populations that are radio collared after intensive efforts to catch a majority of individuals present remain the best method for calculating population estimates and trends (Rinehart et al. 2014). We tested the idea that collaring every lion within or near a particular geographic area is the most meaningful method to determine population density and trend if the proportional amount of radio telemetry data for each individual within that geographic area is considered. Further, we compared the results of two indices derived from that method.

Materials and Methods

Study area.—Round Valley (118° 28' W, 37° 28' N), located east of the Sierra Nevada in eastern California, is the winter range for a migratory population of mule deer, and the mountain lions that prey upon them (Kucera 1988, Pierce et al. 2004, Monteith et al. 2011, B. M. Pierce et al. 2012, Monteith et al. 2014). Mean monthly temperatures range from 8° C to 16.8° C. The predominant vegetation type in Round Valley is sagebrush steppe (Pierce et al. 2004), characteristic of the western Great Basin.

Methods.—During 1991–2007 we used hounds or snares to capture mountain lions that used the Round Valley winter range and, beginning in 2000, individuals throughout the eastern Sierra Nevada including Round Valley, for the purpose of protecting Sierra Nevada bighorn sheep (*Ovis canadensis sierrae*), an endangered taxon (USFWS 2007). We considered any mountain lion that was no longer dependent on its mother to be an adult. We conducted regular and intensive searches for mountain lions throughout the study area during 1991–2007. These intensive searches provided strong evidence that all mountain lions that used the winter range in Round Valley were fitted with radio collars by 1993, a situation that remained constant throughout our investigation. Detailed descriptions of searches for mountain lions and mule deer killed by predators were provided previously by Pierce et al. (1998, 2000a, 2000b; B. M. Pierce et al. 2012).

We focused our efforts for this study during winter because we were interested in the impacts of mountain lion predation on mule deer and bighorn sheep on winter ranges. Both species use concentrated areas in Round Valley during winter; additionally, we discovered that during summer, some mountain lions made long distance movements, following the migrating mule deer to the west side of the Sierra Nevada, or moved east to other mountain ranges (Pierce et al. 1999) . Those long distance movements made collecting location data more difficult, and expanded the study area causing it to overlap a much larger number of unmarked mountain lions. Therefore, the core area was representative of the collared mountain lions using winter ranges but not summer ranges.

We developed the fixed wing index prior to the availability of GPS radio collars for mountain lions. Following the deployment of GPS collars on mountain lions in 1998 (Bleich et al. 2000), we continued with the fixed wing flights and were able to compare that index to one using the proportion of locations from VHF data alone (fixed wing index) and combined VHF and GPS data (location data index). We determined the mean number of collared mountain lions on the study area during telemetry flights at weekly intervals from November to April each year, and used that value to index the number of adult mountain lions on the winter range annually. We excluded winter 1991–1992, because we captured the first mountain lion during December 1991 and continued to capture new, unmarked lions in Round Valley until November 1992, by which time we had captured 12 adults. From then on, our intensive effort to detect and capture new, unmarked lions was constant from year to year (Pierce et al. 2000a, 2000b). All research methods were approved by an independent Animal Care and Use Committee at the University of Alaska Fairbanks, and complied with guidelines published by the American Society of Mammalogists for research on wild mammals (Committee on Acceptable Field Methods 1987).

We delineated a 450 km^2 core area within the intensively hunted Round Valley study area (Figure 1). Fixed-wing telemetry flights for mountain lions emphasized locating all animals known to use the core area in Round Valley. We used the same pilots and aircraft as those used by Nicholson et al. (1997) and Oehler et al. (2004), and location error (±170 m) was small (12.5 ha) compared to the size of the core area (450 km^2).We plotted locations using ArcView 9.3, and the number of adult mountain lions located within the core area during each weekly flight was averaged for each winter. The average number of mountain lions located within the core area during telemetry flights constituted the fixed wing index for each year. Concurrently, location data from combined aerial telemetry and GPS collar locations for adult mountain lions known to use the core area were plotted. The proportion of locations that landed within the core area during winter was calculated for

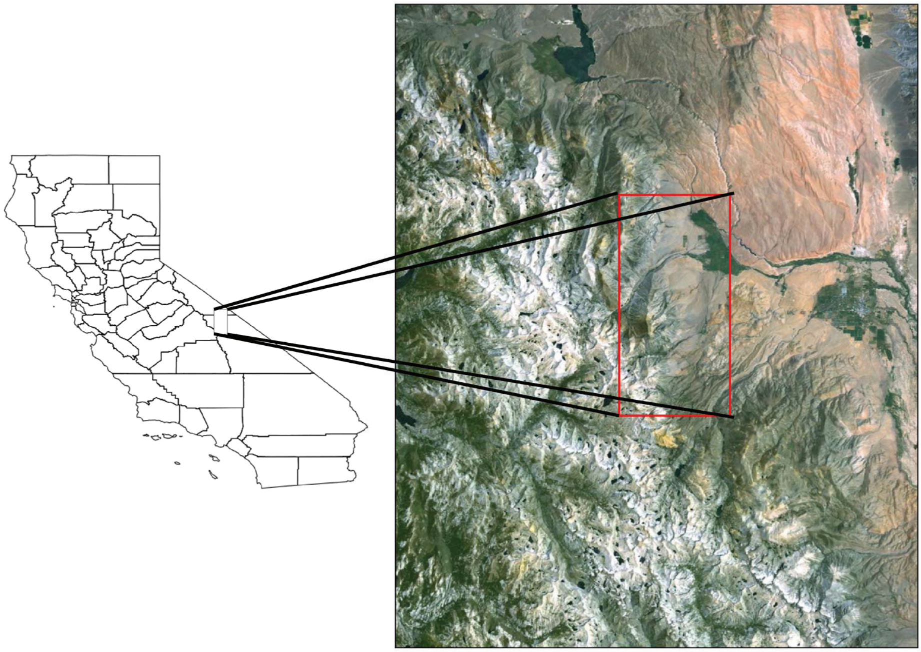

Figure 1.—The study area and pre-defined core area encompassing Round Valley (118° 28' W, 37° 28' N), Inyo and Mono counties, California, that was established to develop indices to the number of mountain lions (*Puma concolor*) present in the core area each winter from 1993 to 2007, as described in this paper.

each individual, and those proportions were summed to produce the location data index. For example if there was a total of two mountain lions known to use the core area during a particular winter, a mountain lion with 50% of its total locations within the core area and a mountain lion with all of its locations in the core area, the first lion would receive a score of 0.5, while the second would receive a score of 1.0. Those values would then be summed, yielding a location data index of 1.5 mountain lions for the winter.

We tested for association between the indices over 15 years (1993–2007) with the Spearman Rank Correlation Coefficient (ρ; Siegel 1956). We used a 2-tailed Wilcoxon Matched-Pairs Signed-Ranks Test (*W*; Siegel 1956) to compare changes in index values in the estimated numbers of mountain lions present in the defined area based on aerial telemetry methods (e.g., $FWI_{1994} – FWI_{1993}$) and estimates based on proportion of use each year (e.g., $LDI_{1994} – LDI_{1993}$) over 14 winters from 1994 to 2007 (Table 1). We set α=0.05, and performed statistical tests using VassarStats (Lowery 2014). We present the test statistic and associated probability derived from each test, as well as the equivalent t-value or z-value and associated probability, as calculated by Lowery (2014).

Table 1.—Number of collared mountain lions each winter known to have used a core area at least once, mean number of lions present and standard error (*SE*) derived from aerial telemetry during winter, and the cumulative proportion of mountain lions present each winter in the predefined area of 450 km^2 encompassing Round Valley, Inyo and Mono counties, California, 1993–2007.

Year	Available lions (N)[a]	Fixed-wing Index(SE)[b]	Location Data Index[c]
1993	10	6.09 (0.744)	7.56
1994	9	5.83 (0.599)	4.56
1995	8	5.38 (0.195)	5.15
1996	5	4.27 (0.258)	3.23
1997	4	2.80 (0.159)	2.31
1998	4	2.29 (0.187)	2.51
1999	2	1.17 (0.150)	0.56
2000	3	1.77 (0.210)	2.83
2001	3	1.62 (0.260)	1.63
2002	4	1.70 (0.272)	2.05
2003	3	1.30 (0.200)	1.56
2004	3	1.00 (0.150)	1.27
2005	6	2.27 (0.260)	3.41
2006	6	1.82 (0.280)	1.97
2007	3	1.57 (0.190)	2.26

[a]Number of collared lions collared in the study area each winter that were known to have used the core area at least once
[b]Aerial index of lions and standard error using the core area each winter
[c]Location data index of lions using the core area each winter

Results

We captured and collared 29 adult mountain lions (16 females, 13 males) that used Round Valley during this investigation and fitted each with a very high frequency (VHF) radio collar or various models of GPS collars. Values for the average number of adults located within the study area during aerial telemetry flights in winter varied from 1.0 to 6.1 (Table 1). Values for the summed proportion of locations for each adult mountain lion within the core area varied from 0.6 to 7.6 (Table 1). We evaluated the relationship between these two indices over a period of 15 years, and the results were strongly correlated (ρ=0.907, P<0.001 [t=7.770, P<0.001]; Figure 2). Successive interannual changes in the fixed wing index compared to those determined from the location data index did not differ (W=1, P>0.05 [z=-0.020, P=0.984]). The two indices trended in the same direction for 12 of 15 years, and the sizes of both indices were remarkably similar.

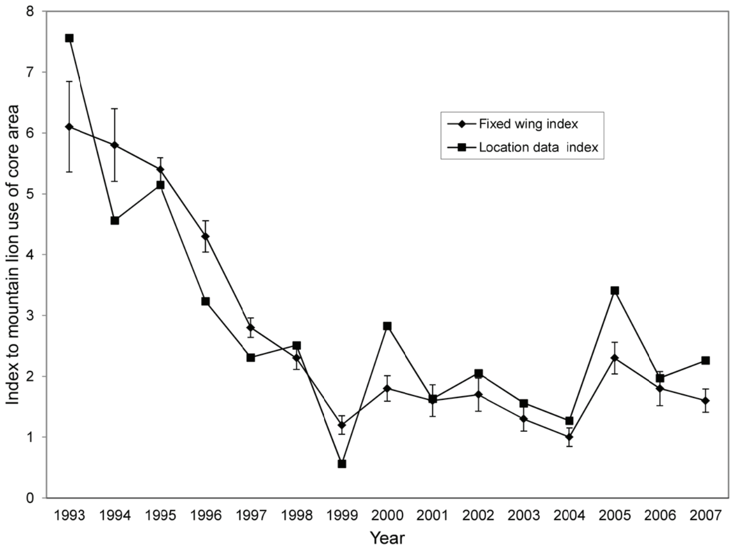

Figure 2.—Fixed-wing index (±*SE*) to the number of mountain lions determined from aerial telemetry locations, and the location data index, which was determined by summing the proportional use of all locations for mountain lions present on the pre-defined core area within the study area encompassing Round Valley (118° 28' W, 37° 28' N), Inyo and Mono counties, California each winter from 1993 to 2007.

Discussion

We used two different indices to assess the number of mountain lions using a specified area of deer winter range. We recognized that other methods did not account for proportional use of an area by individual animals, and they do not provide an opportunity to create a variance around mean estimated density. Methods such as minimum counts based on tracks or location data substantially inflate the actual use of a specified area, as well as the number of individuals present if more than one area is being evaluated. For example, a mountain lion that spent one day on a specified area and then moved to another for the rest of the time would be counted as one lion in each of those areas, essentially doubling the count and greatly inflating the estimate of the number of lions using an area where that individual rarely occurred. For states where mountain lions are hunted, population counts and estimates are often calculated for relatively small management units compared to the extensive movements made by mountain lions, further exacerbating the problem.

Our methods are based on the proportional use of an area by each individual. Further, the probability of detecting a mountain lion present in the defined area through the use of aerial telemetry was essentially 100%, particularly if the individual could be accounted for outside the defined area, and obviated one of the shortcomings voiced by Anderson (2003). Moreover, despite the fact that GPS locality data are not always indisputable (Villepique et al. 2008) and that not every attempted location by a GPS collar is successful (Cain et al. 2005), it reasonable to assume that the probability of detecting a telemetered individual within the defined area approaches 100%. Therefore, the density of mountain lions during any given period can be estimated while accounting for individuals that are present only occasionally.

Both indices described here yielded very similar results (Figure 2). Further, our methods allowed us to visualize actual use of the core area for any given period. We recognized that there were a number of individuals that used the study area only occasionally, and that it would be unlikely that the total number of individuals identified as using it, or any other area, would all be present on any given day.

Despite the close agreement between the indices, our results potentially remain subject to the effects of extrapolation bias and area bias, as described by Rinehart et al. (2014). The scale at which densities are defined will remain problematic, regardless of the accuracy or precision associated with density estimates (e.g., Blackburn and Gaston 1996, Smallwood and Schonewald 1998, Maffei and Noss 2008), and care must be utilized when extrapolating densities from one area to another (Latham et al. 2014). Nevertheless, for predetermined areas, our method accounts for actual use in proportion to other areas that are used by animals that never leave the predetermined area. Our method also decreases the likelihood that a telemetered mountain lion will be included in density estimates for >1 area without accounting for the proportional use of those areas. Finally, depending on the frequency of aerial telemetry or GPS fixes, a variance can be calculated for mean lion density on a longitudinal scale, whether it is weeks, months, seasons, or years.

Our methods require telemetered animals and, therefore, are not available to all managers tasked with determining mountain lion numbers or assessing population dynamics. We suggest, however, that investigators that do have access to such technology use proportional location data to evaluate use of subset areas for species that exist in a continuous population beyond the defined boundaries of their study areas. Additionally, we encourage incorporating a temporal component when seasons cause significant variation in study area size or location data accuracy. Finally, we suggest that the selection of a smaller area that is representative of larger areas can be used to estimate population trends in a meaningful way using these methods. Managers should recognize that censuses determining only the total number of individuals that have been identified in an area often inflate the total number of individuals likely to be present in that area at the same time, potentially leading to erroneous conclusions and, in jurisdictions where offtake is high (road kills, depredation, harvest), overestimates could mask actual population declines.

Acknowledgments

We thank J. Davis and J. Ostergard for the capture and handling of mountain lions, and C. Baker, J. Constible, V. Davis, M. Kiner, M. Leonard-Cahn, K. Moore, S. Mussulman, S. Overholt, P. E. Partridge, J. Schmalenberger, D. Stoner, and J. Villepique for assisting with mountain lion captures and data collection. P. E. Partridge, C. Baker, and W. J. Allsup, also served as observers during fixed-wing telemetry flights, and we thank pilots R. W. Anthes and G. Schales for the dozens of flights they conducted. We thank K. Mayer, E. Loft, S. Torres, and T. Mansfield for administrative support, and the National Rifle Association Foundation, Fish and Game Advisory Committee of Inyo and Mono Counties, California Deer Association, Mule Deer Foundation, and the California Department of Fish and Game Deer Herd Management Plan Implementation Program for funding this research. We thank D. Stoner, an anonymous reviewer, and Guest Editor S. Osborn for numerous suggestions that resulted in many improvements to the manuscript. During manuscript preparation, V. C. Bleich was supported by the Eastern Sierra Center for Applied Population Ecology (ESCAPE); this is Professional Paper 105 from ESCAPE.

Literature Cited

Anderson, D. R., 2001. The need to get the basics right in wildlife field studies. Wildlife Society Bulletin 29:1294-1297.

Anderson, D. R. 2003. Response to Engeman: index values rarely constitute reliable information. Wildlife Society Bulletin 31: 288-291.

Andreasen, A. M., K. M. Stewart, W. S. Longland, J. P. Beckman, and M. L. Forister.. 2012. Identification of source-sink dynamics in mountain lions of the Great Basin. Molecular Ecology 21:5689-5701.

Blackburn, T. M., and K. J. Gaston. 1996. Abundance-body size relationships: the area you census tells you more. Oikos 75:303-309.

Bleich, V. C., B. M. Pierce, S. G. Torres, and T. Lupo. 2000. Using space age technology to study mountain lion ecology. Outdoor California 61(3):24-25.

Bowyer, R. T., D. K. Person, and B. M. Pierce. 2005. Detecting top-down verses bottom–up regulation of ungulates by large carnivores: implications for conservation of biodiversity. Pages 342-361 *in* J. C. Ray, K. H. Redford, R. S. Steneck, and J. Berger, editors. Large carnivores and the conservation of biodiversity. Island Press, Washington, D.C., USA.

Cain, J. W. III, P. R. Krausman, B. D. Jansen, and J. R. Morgart. 2005. Influence of topography and GPS fix interval on GPS collar performance. Wildlife Society Bulletin 33:926-934.

Choate, D. M., M. L. Wolfe, and D. C. Stoner. 2006. Evaluation of cougar population estimators in Utah. Wildlife Society Bulletin 34:782-799.

Committee on Acceptable Field Methods. 1987. Acceptable field methods in mammalogy. Journal of Mammalogy 68(supplement):1-18.

Cougar Management Guidelines Working Group. 2005. Cougar management guidelines. Wild Futures, Bainbridge Island, Washington, USA.

Engeman, R. M. 2003. More on the need to get the basics right: population indices. Wildlife Society Bulletin 31:286-287.

Ernest, H. B, M. C. T. Penedo, B. P. May, M. Syvanen, and W. M. Boyce. 2000. Molecular tracking of mountain lions in the Yosemite Valley region in California: genetic analysis using microsatellites and fecal DNA. Molecular Ecology 9:433-441.

Ernest, H. B., W. M. Boyce, V. C. Bleich, B. M. May, S. J. Stiver, and S. G. Torres. 2003. Genetic structure of mountain lion (*Puma concolor*) populations in California. Conservation Genetics 4:353-366.

Grigione, M. M., P. Burman, V. C. Bleich, and B. M. Pierce. 1999. Identifying individual mountain lions (*Felis concolor*) by their tracks: refinement of an innovative technique. Biological Conservation 88:25-32.

Hemker, T. P., F. G. Lindzey, and B. B. Ackerman. 1984. Population characteristics and movement patterns of cougars in southern Utah. Journal of Wildlife Management 48:1275-1284.

Hughson, D. L., N. W. Darby, and J. D. Dungan. 2010. Comparison of motion-actuated cameras for wildlife investigations. California Fish and Game 96:101-109.

Jenks, J. A. (editor). 2011. Managing cougars in North America. Jack H. Berryman Institute, Utah State University, Logan, USA.

Logan, K. A., and L. L. Sweanor. 2001. Desert puma: evolutionary ecology and conservation of an enduring carnivore. Island Press, Washington, D.C., USA.

Long, E. S., D. M. Fecske, R. A. Sweitzer, J. A. Jenks, B. M. Pierce, and V. C. Bleich. 2003. Efficacy of photographic scent stations to detect mountain lions. Western North American Naturalist 63:529-532.

Kucera, T. E. 1988. Ecology and population dynamics of mule deer in the eastern Sierra Nevada, California. Ph.D. Dissertation, University of California, Berkeley, USA.

Latham, M. C., M. D. M. Latham, N. F. Webb, N. A. McCutchen, and S. Boutin. 2014. Can occupancy abundance models be used to monitor wolf abundance? PLoS ONE 9(7): e102982. doi:10.1371/journal.pone.0102982

Lowery, R. 2013. [Internet] Concepts and applications of inferential statistics. Accessed 1 December 2014. Available at www.vassarstats.net

Maffei, L., and A. J. Noss. 2008. How small is too small? Camera trap survey areas and density estimates for ocelots in the Bolivian Chaco. Biotropica 40:71-75.

McBride, R. T., R. T. McBride, R. M. McBride, and R. E. McBride. 2008. Counting pumas by categorizing physical evidence. Southeastern Naturalist 7:381-400.

McDonald, L. L. 2004. Sampling rare populations. Pages 11-42 *in* W. L. Thompson, editor. Sampling rare or elusive species: concepts, designs and techniques for estimating population parameters. Island Press, Washington, D.C., USA.

Monteith, K. M., V. C. Bleich, T. R. Stephenson, B. M. Pierce, M. M. Conner, R. W. Klaver, and R. T. Bowyer. 2011. Timing of seasonal migration in mule deer: effects of climate, plant phenology, and life-history characteristics. Ecosphere 2(4):art47. DOI:10.1890/ES10-00096.1

Monteith, K. M., V. C. Bleich, T. R. Stephenson, B. M. Pierce, M. M. Conner, J. G. Kie, and R. T. Bowyer. 2014. Life history characteristics of mule deer: effects of nutrition in a variable environment. Wildlife Monographs 186:1-63.

Munoz-Pedreros, A., J. R. Rau, M. Valdebenito, V. Quintana, and D. D. Martinez. 1995. Relative density of pumas (*Felis concolor*) in a forestry ecosystem of southern Chile. Revista Chilena de Historia Natural 68:501-507.

Pierce, B. L., R. R. Lopez, and N. J. Silvy. 2012. Estimating animal abundance. Pages 284-310 *in* N. J. Silvy, editor. The wildlife techniques manual – research. Seventh edition, volume 1. Johns Hopkins University Press, Baltimore, Maryland, USA.

Pierce, B. M., and V. C. Bleich. 2003. Mountain lion. Pages 744-757 *in* G. A. Feldhamer, B. C. Thompson, and J. A. Chapman, editors. Wild mammals of North America: management and conservation. Second edition. Johns Hopkins University Press, Baltimore, Maryland, USA.

Pierce, B. M., V. C. Bleich, and R. T. Bowyer. 2000a. Selection of mule deer by mountain lions and coyotes: effects of hunting style, body size, and reproductive status. Journal of Mammalogy 81:462-472.

Pierce, B. M., V. C. Bleich, and R. T. Bowyer. 2000b. Social organization of mountain lions: does a land-tenure system regulate population size? Ecology 81:1533-1543.

Pierce, B. M., V. C. Bleich, K. L. Monteith, and R. T. Bowyer. 2012. Top-down versus bottom-up forcing: evidence from mountain lions and mule deer. Journal of Mammalogy 93:977-988.

Pierce, B. M., V. C. Bleich, J. D. Wehausen, and R. T. Bowyer. 1999. Migratory patterns of mountain lions: implications for social regulation and conservation. Journal of Mammalogy 80:986-992.

Pierce, B. M., R. T. Bowyer, and V. C. Bleich. 2004. Habitat selection by mule deer: forage benefits or risk of predation? Journal of Wildlife Management 68:533-541.

Rinehart, K. A., L. M. Elbroch, and H. U. Wittmer. 2014. Common biases in density estimation based on home range overlap with reference to pumas in Patagonia. Wildlife Biology 20:19-26.

Seidensticker, J. C., IV, M. G. Hornocker, W. V. Wiles, and J. P. Messick. 1973. Mountain lion social organization in the Idaho Primitive Area. Wildlife Monographs 35:1-60.

Siegel, S. 1956. Nonparametric statistics for the behavioral sciences. McGraw-Hill Book Company, New York, USA.

Sinclair, E. A., E. L. Swenson, M. L. Wolfe, D. M. Choate, B. Bates, and K. A. Crandall. 2001. Gene flow estimates in Utah's cougars imply management beyond Utah. Animal Conservation 4:257-264.

Smallwood, K. S., and C. Schonewald. 1998. Study design and interpretation of mammalian carnivore density estimates. Oecologia 113:474-491.

Stoner, D. C., M. L. Wolfe, and D. M. Choate. 2006. Cougar exploitation levels in Utah: implications for demographic structure, population recovery, and metapopulation dynamics. Journal of Wildlife Management 70:1588-1600.

USFWS (U.S. Fish and Wildlife Service). 2007. Recovery plan for the Sierra Nevada bighorn sheep. U.S. Fish and Wildlife Service, Sacramento, California, USA.

Villepique, J. T., V. C. Bleich, R. A. Botta, B. M. Pierce, T. R. Stephenson, and R. T. Bowyer. 2008. Evaluating GPS collar error: a critical evaluation of Televilt POSREC-Science™ Collars and a method for screening location data. California Fish and Game 94:155-168.

Walker, C. W., L. A. Harveson, M. T. Pittman, M. E. Tewes, and R. L. Honeycutt. 2000. Microsatellite variation in two populations of mountain lions (*Puma concolor*) in Texas. Southwestern Naturalist 45:196-203.

Received 12 November 2014
Accepted 23 December 2014
Guest Editor was S. Osborn