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Population Ecology

Bear Historical Ranges Revisited: Documenting the Increase of a Once-Extirpated Population in Nevada

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ABSTRACT Black bears (*Ursus americanus*) were once abundant in Nevada and distributed throughout the state, yet recognition of the species' historical occurrence in the state is uncommon and has therefore been ignored in published distribution maps for North America. The lack of representation on distribution maps is likely due to the lack of any scientific data or research on bears in Nevada until 1987. Historical records dating back to the 1840s compiled by Nevada Department of Wildlife (NDOW) biologist Robert McQuivey indicate presence of black bears throughout the state in the 1800s through about 1930. The paucity of historical references after 1931 suggest extirpation of black bears from Nevada's interior mountain ranges by this time. We report on historical records of black bears in the state of Nevada and the results of a current population estimate of black bears derived from a sample of marked bears ($n = 420$) captured 707 times between 1997 and 2008. Using Pradel and Cormack–Jolly–Seber models in Program MARK, we estimated overall population size, finite rate of growth ($\lambda = 1.16$), quarterly and annual survival rates for males and females, seasonal capture probabilities, and recruitment rates. Our results indicate an overall population size of 262 ± 31 adult black bears in western Nevada. These results suggest that the once abundant, then extirpated population of black bears in Nevada is increasing at an annual average rate of 16%. Although the current distribution is limited to the western part of the state, our findings suggest possible expansion of the population into historical habitat within the interior and eastern portions of the state that have been absent of bears for >80 years. Finally, based on historical records, we present suggested revised historical distribution maps for black bears that include the Great Basin ranges in Nevada.

KEY WORDS black bear, extirpated population, historical records, Nevada, population estimation, *Ursus americanus*.

Conflicts between humans and black bears (*Ursus americanus*) have increased in North America (Gore et al. 2005, Hristienko and McDonald 2007) and in Nevada, where a 10-fold increase in the number of complaints and a 17-fold increase in bear mortalities due to collisions with vehicles were reported between the early 1990s and mid-2000s (Beckmann and Berger 2003*a*). In 1997, motivated by these increasing bear–human conflicts, but without knowing what catalyst was driving the increase, we began a long-term study of Nevada's black bears that continues to present. Nevada Department of Wildlife (NDOW) needed to know if the increase in complaints was due to an increasing or expanding bear population, or a redistribution of the existing bear population into the urban interface. These questions were important to managers, in part, because this phenomenon of increasing human–bear conflicts was not the case in Nevada just less than 3 decades ago. Furthermore, if the population is increasing, managers should have reliable estimates of abundance on which to make management recommendations, such as a legal harvest. Additionally, if the bear population is expanding into formally occupied habitat, then our results would provide the context on which NDOW could make decisions regarding where occupancy by black bears is desirable.

Prior to the late 1980s, bear sightings and bear deaths from vehicles were considered such a rare event (Goodrich 1993) that the then director of the NDOW made the statement at the First Western Black Bear Workshop, "Nevada has no bear, except for an occasional one that strays in along the Sierras adjacent to Lake Tahoe in California. Therefore, we have no management responsibilities" (LeCount 1979:63). Yet, historical records from newspapers and pioneer journals dating to 1849 (McQuivey 2004; see Appendix) indicate presence of American black bears in all of their current range (Lackey 2004) and in the interior mountain ranges of Nevada. Unfortunately, this historical information has never been disseminated outside the NDOW and therefore the historical range of this species in Nevada has never been fully represented in the published literature (e.g., Hall 1981, Pelton and van Manen 1994, Servheen et al. 1999; Fig. 1).

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We analyzed historical newspaper and journal accounts of black bears to illustrate their distribution throughout the state and their consequent extirpation from all but the far western part of Nevada. We used these records to suggest revised historical range maps for black bears in North America, a more accurate representation of this species' historical distribution. Furthermore, we used an extensive 12-year data set to estimate current population size and rate of population change for the black bear population in Nevada. Finally, we overlaid recent sightings of black bears from 1988—present onto a map of historical habitat to show that this population increase is resulting in expansion of the species into areas of the Great Basin that have been unoccupied by black bears for >80 years.

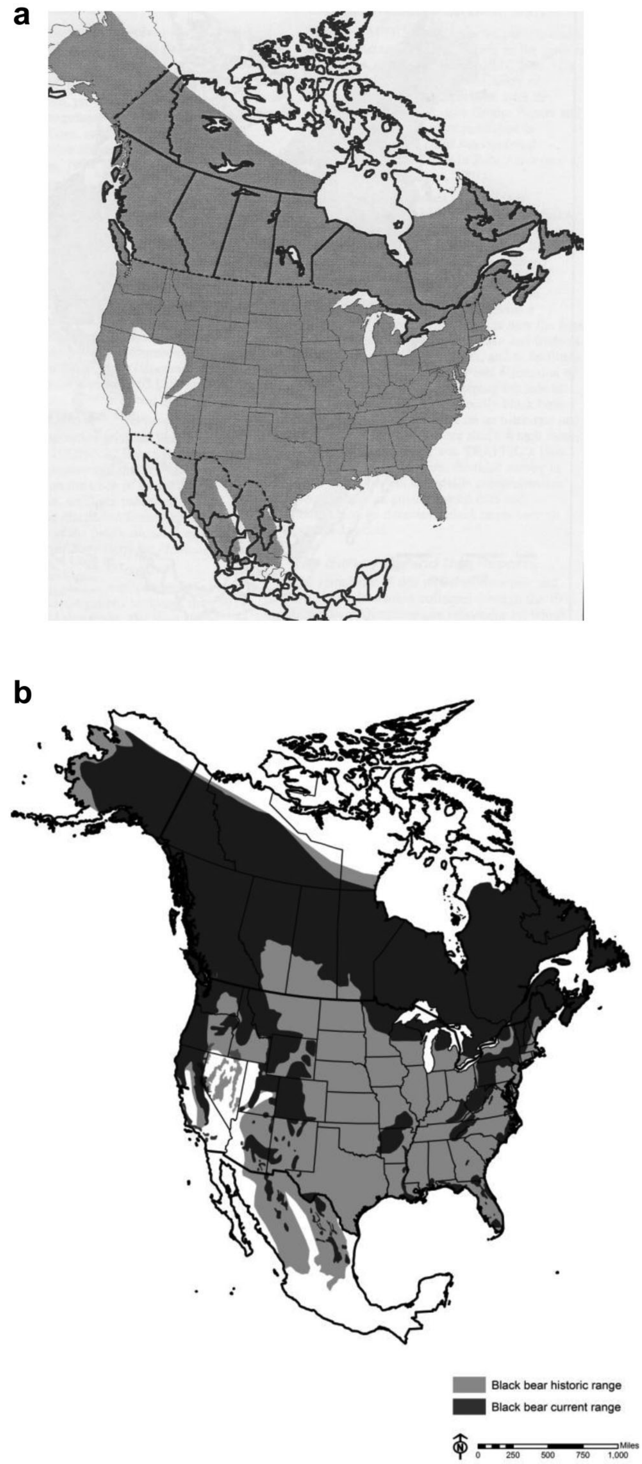

Figure 1. (a) Historical distribution of the American black bear (*Ursus americanus*) in North America. Modified from Hall (1981). (b) Revised historical distribution map and current distribution map of American black bear in North America based on our data from Nevada. Modified from Pelton and van Manen (1994).

STUDY AREA

The current distribution of black bears in Nevada is restricted to the Carson Range of the Sierra Nevada, Pine Nut Range, Pine Grove Hills, Sweetwater Range, Virginia Range, and the Wassuk Range in western Nevada (Beckmann and Berger 2003*a*; Lackey 2004; NDOW, unpublished data). These 6 mountain ranges and associated basins cover an area of approximately 12,065 km^2 and are characterized by steep topography with high granite peaks and deep canyons. Mountain ranges are separated by desert basins that range from 15 to 64 km across (Grayson 1993). These basins are often large expanses of unsuitable habitat (e.g., large areas of sagebrush [*Artemisia* spp.]) that bears do not use as primary habitat (Goodrich 1990, Beckmann and Berger 2003*a*). For the population demographics portion of our analysis, the study area extended from the Carson Range of the Sierra Nevada eastward to the Virginia Range and Pine Nut Mountains, and from Reno south to Topaz Lake, an area collectively referred to as the Carson Front. Additionally, because many captures were in response to conflicts (see the Methods Section), the urban-interfaces of cities and towns within the study area were represented as well and included developed areas in the Lake Tahoe Basin: Incline Village, Glenbrook, Cave Rock, Zephyr Cove, and Stateline, Nevada, and the lower elevation urban centers of Reno, Carson City, Minden, and Gardnerville and their associated valleys. Even though human–bear conflicts increased in number over the period of our study (1997–2008), the geographic distribution of those conflicts did not change and therefore the study area itself remained consistent. The expanding geographic distribution of black bears is occurring concurrently with the increasing bear population, but it is occurring beyond the study area boundaries defined above for the population demographics portion of our study.

METHODS

Historical Distribution

We analyzed historical newspaper records and pioneer journals with notation of bears from 1833 to 1964 and categorized them as either black bear or grizzly bear (*Ursus arctos*) as both species are recognized in the records. Intended species for some records (14%) was clear based on use of the terms "grizzly bear," "brown bear," or "black bear." Nine percent of records used the term "cinnamon bear," which we interpreted as black bear records in all instances ($n = 27$) except 1. Seventy-seven percent of the records were not specific to species ($n = 237$), but in every case except 2 we categorized them as black bears. We mapped historical distribution of black bear in Nevada using geographic information system (GIS) software (ArcGIS Desktop 10, Environmental Systems Research Institute, Inc., Redlands, CA) to overlay the historical sighting records with 8-digit hydrologic unit code (HUC) watershed polygons. Thus, we interpreted black bear historical range areas to be those watersheds that contained historical sighting records (Fig. 2). We also documented and mapped every sighting since 1988 of a bear or bear sign outside of their currently recognized range (Lackey 2004). We relied on confirmed sightings of bears, bear tracks, or scat by NDOW biologists, other agency personnel such as United States Department of Agriculture Animal and Plant Health and Inspection Service (APHIS) Wildlife Services, or in some cases 2 or more hunters reporting the same sighting. Additionally, we had information from bears captured from 1988 to present within the historical range. We plotted these points on a map illustrating possible expansion of black bears into historical habitat (Fig. 2).

Field Methods

We captured bears using culvert traps (Teton Welding, Choteau, MT), modified Aldrich foot snares, and free-range techniques (i.e., tranquilizing unconfined animals). We captured bears in response to ongoing conflict complaints (urban-interface bears) as received from NDOW dispatch or through direct communications with complainants, and in remote areas absent of conflicts (wildland bears) as described in Beckmann and Berger (2003*a*). We captured bears year-round to the extent that some urban-interface bears did not enter dens during the winter months (Beckmann 2002). Per NDOW conflict policy (NDOW 1998), we either released captured bears on-site (point of capture) or we relocated them to areas within their home range. On 8 occasions, we translocated marked bears to other areas within the study area (Beckmann and Lackey 2004); however, on every one of these occasions, the bear returned to the capture site in 18 days or less.

We tranquilized bears with a mixture of 4.4 mg/kg Telazol® (Fort Dodge Animal Health, Fort Dodge, IA) and 2.2 mg/kg xylazine. We assigned a unique identification number to each bear that we captured and released and marked each bear with a corresponding ear tag (AllFlex USA, Inc., TX) and lip tattoo. Dates of capture were from 27 June 1997 to 26 November 2008. Additionally, we recorded all known mortalities during the course of the study. For every capture or mortality event, we recorded date of handling, sex, age, weight, color, physical condition, reproductive status, and various morphological measurements. We pulled 1 tooth, either the first or second premolar (PM1 or PM2) to determine age of the bear (Matson's Laboratory, Milltown, MT; Stoneberg and Jonkel 1966) and classified animals as dependant young (<1.5 years), juveniles (1.5–3 years), or adults (>3 years).

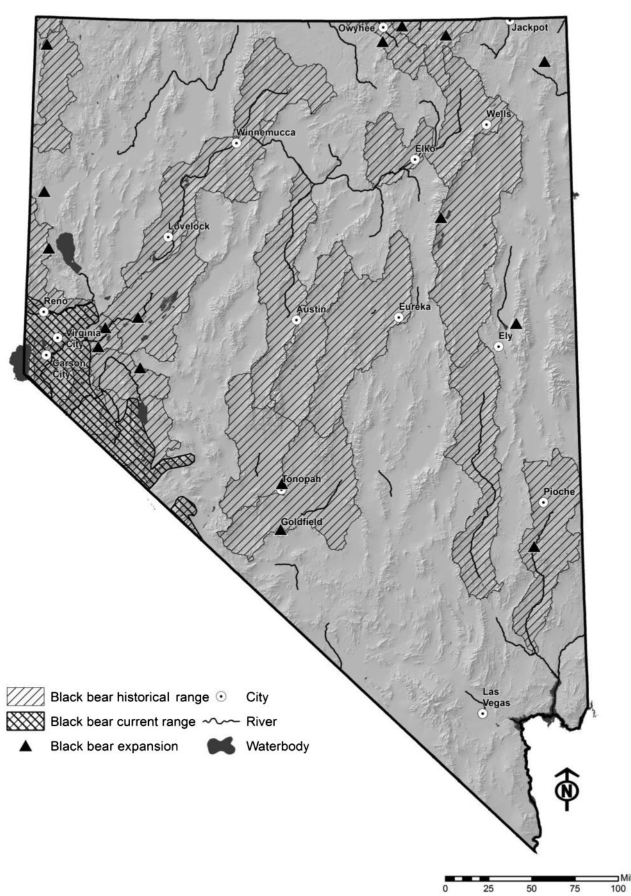

Figure 2. American black bear (*Ursus americanus*) historical (from McQuivey 2004) and current distribution in Nevada, and recent sightings (1988–2012) of black bear indicating possible expansion into historical range that has been unoccupied for >80 years. Historical black bear range was developed by overlaying historical sighting records with 8-digit hydrologic unit code watershed polygons.

Population Demographics

We used captures of individually marked bears to develop capture histories, which we used to perform 2 analyses: 1) a Cormack–Jolly–Seber (CJS) analysis (Cormack 1964, 1989; Jolly 1965; Seber 1965, 1986) and 2) a Pradel analysis (Pradel 1996). Pradel models use capture histories analyzed in both the typical forward direction and in the backward direction to estimate capture probability (P), survival (ϕ), seniority (the probability an individual captured on a given occasion was present in the population before that occasion), and λ (per capita rate of population change; Pradel 1996). Pradel (1996) models require the same assumptions as are required by Cormack–Jolly–Seber capture-mark methods, including the assumption that individuals have identical capture and survival probabilities and independent fates. Pradel models also assume that marked and unmarked animals are equally likely to be captured. Because capture histories were sparse, we consolidated monthly capture occasions ($n = 138$) into seasonal capture occasions ($n = 44$) and recorded captures (or lack thereof) for each individual bear for each season: winter (1 Dec–28 Feb), spring (1 Mar–31 May), summer (1 Jun–31 Aug), and fall (1 Sep–30 Nov). We did not use annual encounter histories because doing so would violate the assumption of instantaneous sampling. Violation of this assumption introduces heterogeneity into survival probabilities because individuals captured near the beginning of an occasion have a lesser probability of surviving to the next occasion than individuals captured near the end of an occasion. This is because the former group is exposed to mortality for a longer period than the latter group. We violated this assumption by using 3-month sampling intervals; however, we felt that the 3-month intervals we used represented the best balance between the assumption of instantaneous sampling and producing capture histories with sufficiently high capture probabilities. Using seasonal capture occasions also captured seasonal variation in bear activity, survival, and capture probabilities.

We used the Pradel model structure in Program MARK (White and Burnham 1999) to estimate seasonal capture probabilities, survival, and λ. Because capture histories had a seasonal structure and we were interested in annual estimates of λ, we constrained 3 of the 4 seasonal estimates of λ to equal 1.0 so the product of the 4 seasonal estimates produced an annual estimate of λ. We allowed estimates of survival, capture probability, and λ to vary between the sexes. We also allowed estimates of capture probabilities to vary among seasons. Models that allowed survival, capture probability, or λ to vary among years of the study did not converge, likely because of the sparseness of the data. Our estimates of parameters, therefore, represent averages across the years of the study.

Pradel and CJS models generally require similar assumptions as other capture-mark-recapture approaches (Pradel 1996). In these models, animals are assumed to be identical and to have independent fates. We also assumed that marks were not lost. Differentiating emigration out of the study area from mortality of individuals was not possible; therefore, survival estimates represent apparent survival. Although conflicts increased during certain seasons (summer and fall), the geographic area of these captures did not change over the course of the population demographics portion of our study. Further, we removed 62 dependent cubs from the analysis because we restricted encounter histories to individuals >16 months old. Our estimates of λ, therefore, refer to the adult portion of the population only. We estimated total population size as the sum of CJS estimates of population size for female and male bears.

We calculated $\hat{c}$ using the bootstrap goodness-of-fit procedure in Program Mark to account for heterogeneity in capture and survival probabilities and adjusted second-order Akaike's Information Criterion (AIC_c) scores accordingly. We therefore report quasi-likelihood AIC_c ($QAIC_c$) scores. We report model-averaged parameter estimates from both the Pradel and CJS analyses. We used the delta method (Powell 2007) to calculate standard errors of estimates of annual survival and population size.

RESULTS

Historical Distribution Records

Historical records of bears analyzed ($n = 308$) included 278 black bear records occurring throughout the state. We produced a map illustrating the historical distribution of black bears (Fig. 2) that we suggest as a revision (see Fig. 1b) to the published maps of the historical distribution of this species in North America (Fig. 1a). We plotted sightings of black bears ($n = 12$) and captures ($n = 4$) from 1988 to present that occurred within our historical range polygons but from regions not currently thought to contain resident bear populations in Nevada, illustrating possible geographic expansion of the species into historical habitat (Fig. 2).

Population Demographics

We encountered 420 individual black bears during 707 capture events throughout the study. Of these 420 bears, we first encountered 161 as mortalities (hit by cars, management kills, etc.) and 62 were dependent offspring (≤15 months); therefore, we removed both groups from the analysis. Our capture-mark-recapture analysis, therefore, included the remaining 197 bears (123 males and 74 females) captured a total of 546 times. Bears encountered in the front country (urban-interface) areas accounted for 79% of this total, whereas we encountered 21% in wildland areas, as classified by Beckmann and Berger (2003*a*) and NDOW. These included 19 dependant young males (<1.5 years) captured later as juveniles or adults in the encounter histories, 34 juvenile males (1.5–3 years), and 70 adult males (>3 years); and 16 dependant young females (<1.5 years) captured later as juveniles or adults in the encounter histories, 12 juvenile females (1.5–3 years), and 46 adult females (>3 years).

For the Pradel analysis, no models of capture probability lacking a seasonal structure were competitive ($\Delta QAIC_c >$ 120; Table 1). Model-averaged capture probabilities suggested that males had slightly greater probabilities of capture than females (Table 2). Model-averaged estimates of seasonal survival were 0.968 ± 0.012 for males and 0.959 ± 0.010 for females. Lack of a seasonal structure for survival likely reflected sparseness of our capture data rather than constant survival among seasons.

Table 1. Performance of Pradel models of capture-mark-recapture data for black bears in the Carson Front and Reno-Lake Tahoe area, Nevada, 1997–2008.

Model[a]	$\Delta QAIC_c$[b]	w_i[c]	K[d]	QDeviance[e]
φ(.),*P*(season),λ(.)	0	0.23	6	616.77
φ(S),*P*(season),λ(S)	0.13	0.21	8	612.67
φ(.),*P*(season),λ(S)	0.35	0.19	7	615.01
φ(.),*P*(S + season),λ(S)	0.44	0.18	8	612.98
φ(S),*P*(S + season),λ(S)	1.66	0.10	9	612.06
φ(S),*P*(S + season),λ(.)	1.99	0.08	8	614.53
φ(.),*P*(.),λ(.)	119.97	0	3	742.97
φ(S),*P*(S),λ(S)	121.96	0	6	738.73

[a] Model notation follows Lebreton et al. (1992). φ indicates seasonal survival, *P* indicates seasonal capture probability, and λ indicates rate of population change. S indicates the parameter was allowed to differ between the sexes and season indicates the parameter was allowed to vary among seasons. λ was constrained to 1.0 for 3 of the 4 seasons within each year so the product of the 4 seasonal estimates produced an annual estimate of λ.
[b] Quasi-likelihood second-order Akaike's Information Criterion.
[c] Akaike model weights.
[d] Number of parameters.
[e] Quasi-deviance.

Table 2. Capture probabilities for male and female black bears in the Carson Front and Reno-Lake Tahoe area, Nevada, 1997–2008. Capture probabilities and standard errors are based on model averaged estimates from Pradel models.

	Capture probability (±SE)			
	Summer	Fall	Winter	Spring
Males	0.15 ± 0.02	0.13 ± 0.02	0.02 ± 0.005	0.02 ± 0.005
Females	0.13 ± 0.02	0.11 ± 0.02	0.02 ± 0.005	0.02 ± 0.006

However, products of seasonal survival should represent accurate estimates of annual survival for the 2 sexes. Our estimates of annual survival were 0.88 ± 0.044 for males and 0.85 ± 0.038 for females. Model averaged estimates of λ were 1.21 ± 0.05 for males and 1.14 ± 0.03 for females; indicating that males were increasing 21% per year, whereas females were increasing 14% per year on average.

Only relatively constrained CJS models converged, likely because of the relatively sparse capture histories. The best-supported model allowed survival to differ between the sexes but was otherwise constrained to be constant (Table 3). This model also allowed capture probabilities to vary among seasons and between sexes. This model allowed probability of entry (pent) to vary among seasons, but we constrained all pent to 0 except that for fall. Estimates of seasonal survival and capture probabilities were the same as those from the Pradel analysis. We estimated the global population size within our study area at 262 ± 31 based on our estimate of 171 ± 20 males and 91 ± 11 females.

DISCUSSION

Historical Distribution and Range Expansion

The historical records we analyzed demonstrate that black bear populations in Nevada were once distributed throughout the state, within the Great Basin. Our analysis allowed us to plot these records and illustrate the historical distribution of black bears within the interior of Nevada during the 1800s and into the early 1900s. As such, we suggest that historical range maps for black bears in North America be revised and include the historical records and maps we have produced, which include mountain ranges in the Great Basin. Further, we have shown how these historical records can be useful in documenting the extirpation of a species despite the pitfalls associated with interpreting historical records (Moulton et al. 2010). Although historical records from newspaper accounts can be suspect, such historical records are often used in biological studies and to document historical distributions of species (e.g., see Foster et al. 2002, Hagler et al. 2011). Additionally, these historical records indicate that grizzly bears were present in the Great Basin of Nevada; the last record occurring in 1930, 8 years after grizzly bears were declared extinct in California.

Black bears were probably completely extirpated from the interior mountain ranges of the Great Basin by the first or second decade of the 1900s because of anthropogenic factors. Although over-hunting by pioneers and conflicts with domestic livestock operators likely contributed to this extirpation (Murie 1948, Mattson and Merrill 2002), we suggest that landscape-level changes in patterns of land use also contributed to the extirpation of black bears from Nevada (Goodrich 1990), specifically clear-cutting of forests throughout western and central Nevada (DeQuille 1947, Lord 1883, Nevada Forest Industries Committee 1963). One such example is the Comstock Lode of Virginia City in western Nevada where a 80–96-km swath of the Carson Range in the Sierra Nevada, including the Lake Tahoe Basin in Nevada and California, was clear-cut to supply wood for use in the Virginia City mines (DeQuille 1947, Nevada Forest Industries Committee 1963). The dispensation of this timber would exceed 300 cords of wood every 2 hours at various sawmills processing the logs (Knowles 1942). These clear-cutting practices occurred across the state and resulted in almost total removal of the pinyon-juniper forest canopy in sections of Nevada's interior (Sargent 1879, Young and Budy 1979). Additionally, in western Nevada alone, timber companies cleared over an estimated 190,000 acres in the area around Virginia City, Reno, and Carson City (Young and Budy 1979). As a result, historical records of black bears in western Nevada and in the state's interior declined by the turn of the century. The decline continued until the nation's dependency on fossil fuels increased post World War I; this change combined with changes in forestry practices such as wildfire control, and grazing practices resulted in the slow reforestation of some of these areas (Nevada Forest Industries Committee 1963).

We hypothesize that as this habitat regeneration took place through the 1900s (Young and Budy 1979), black bears slowly increased in abundance in the Carson Range of the Sierra Nevada mountains along the eastern shore of Lake

Table 3. Performance of Cormack–Jolly–Seber models for black bears in the Carson Front and Reno-Lake Tahoe area, Nevada during 1997–2008. Capture histories had a seasonal structure: winter, spring, summer, and fall.

Model[a]	$\Delta QAIC_c$[b]	w_i[c]	K[d]	QDeviance[e]
ϕ(S), P(S + seas), pent(seas), N(S)	0	0.61	10	57.19
ϕ(.), P(S + seas), pent(.), N(S)	0.99	0.37	9	60.34
ϕ(.), P(S + seas), pent(seas), N(S)	7.57	0.01	12	60.40

[a] Model notation as in Lebreton et al. (1992). ϕ indicates seasonal survival, P indicates capture probability, pent indicates probability of entry into the population, and N indicates total population size at the start of the study. Pent was constrained to be 0 except for the fall season to restrict entry to the fall season. S indicates the parameter was allowed to differ between the sexes and seas indicates the parameter was allowed to vary among seasons.
[b] Quasi-likelihood second-order Akaike's Information Criterion.
[c] Akaike model weights.
[d] Number of parameters.
[e] Quasi-deviance.

Tahoe in extreme western Nevada, and by 1987 bears were sufficiently common in western Nevada that NDOW began receiving and annually recording bear–human conflicts. Although we found no record of yearly complaints prior to 1987, complaints rose steadily from 1987 to present and culminated in 2007 at over 1,500. We emphasize that the lack of complaint records prior to 1987 is not because NDOW failed to keep records but rather because bear–human conflicts were almost non-existent (Goodrich 1990, Beckmann 2002). The fact that Nevada's black bear population was ignored in the published literature both geographically (absent from distribution maps) and scientifically (i.e., no rigorous studies of population size or demographics) until the late 1980s has resulted in our knowledge of this population dating back only 25 years. This seemingly rapid reoccupation of western Nevada by black bears resulted in the initiation of the current long-term study of black bears from 1997 to present (e.g., see Beckmann and Berger 2003*a*, *b*; Beckmann and Lackey 2008). Further, California Department of Fish and Game believes their black bear population has grown from an estimated 15,000 in the 1980s to over 38,000 currently, with roughly 32% of these occurring in the Sierra Nevada population along the Nevada-California state line (California Department of Fish and Game-Draft Environmental Document 2011; M. Kenyon, California Department of Fish and Game, personal communication).

Our results suggest that regeneration of the habitat and an increasing population of black bears may be contributing to the geographic expansion of the species into historical habitat in the Great Basin where bears have been absent for >80 years. We documented occupancy in these historical ranges by black bears on at least 16 occasions 1988–2012, and on 4 of these occasions bears were captured. Of the 4 bears captured by NDOW, all were in younger age-classes (2–3 years) and consisted of 3 males and 1 female. Such a small sample makes definite conclusions difficult, but 1 explanation of dispersal of young bears on the edge of their currently known range is an expanding population into unoccupied areas in search of competition-free space (Rogers 1987, Lee and Vaughn 2003, Støen et al. 2006).

Population Demographics

The black bear population in the late 1980s was estimated to be 150–290 when Beckmann (2002) extrapolated from Goodrich's (1990) density estimates to known occupied bear habitat at that time, with a sample of $n = 30$ marked bears. Beckmann and Berger (2003*b*) estimated the population in 2002 at 180 (±117; 95% CI) with a larger sample size ($n = 99$) using closed-capture models in Program MARK. These estimates were within the range calculated from Goodrich's (1990) density data from the late 1980s although direct statistical comparisons were not possible; thus, they did not detect a change in population size based on comparisons between Goodrich's (1990) data and data over the 15-year period from 1987 to 2002 (Beckmann and Berger 2003*b*). Therefore, the conclusion was that the population was not increasing at that time. Using similar mark-recapture techniques and a much larger data set ($n = 197$) from our long-term study (1997–2008), our results indicate a positive rate of change, which we interpreted as a population increase.

We addressed potential violations of key assumptions in our Pradel analysis including trap response bias (capture probability) and we believe data generally met the assumptions. One exception is the assumption that individuals were identical. Biases in estimates of λ become significant when heterogeneity in capture probabilities is large (differences >0.4 between subpopulations of individuals; Hines and Nichols 2002). Our capture probabilities were <0.2 and we therefore believe a trap bias was unlikely. However, we suspect some heterogeneity in capture probabilities because most captures were contingent on individuals having been reported as conflict bears and some individuals were transient in this state. Beckmann (2002) classified bears as conflict or wildland based on behavior characteristics and we noted a change in some bears in these behavioral patterns, particularly later in the study (2006–2008). For example, bears captured during the drought year of 2007 in conflict situations turned out to be wildland bears, based on collar data. However, heterogeneity of capture probability associated with whether bears were conflict or wildland bears does not represent a fundamentally different process than other sources of heterogeneity. Further, heterogeneity in capture probabilities can negatively bias estimates of survival (Pollock and Raveling 1982) and estimates of population size (Otis et al. 1978); therefore, we believe our estimates of population size and λ, if biased, would be low. Our estimate of $\hat{c}$ indicates that heterogeneity and trap response was modest. Our incorporation of $\hat{c}$ into our analyses controlled for any heterogeneity, had it existed.

Additionally, because our trapping effort was largely in response to human–bear conflicts and therefore presumably biased toward male bears, we estimated parameters of capture probability, population size, and λ separately for the 2 sexes. We found only modest support for differences in capture probabilities between the sexes (Table 2). Furthermore, in our study area, male bears were not captured more often than females in conflict situations throughout the entire course of the study, although a male bias in conflict bears occurred early on in the study (1997–2001). This sex bias in conflict bears early on was reported by Beckmann (2002), but it differed by year and in later years of the long-term study it changed from male bears to female bears, particularly in certain years (e.g., 2002, 2004, and 2007; NDOW, unpublished data). Additionally, we doubt our estimates of λ were affected by the male survival rates reported because of the polygamous nature of black bears (Taylor et al. 1987).

Our reported lambdas ($\lambda = 1.21$ and 1.14 for males and females, respectively) are a result of our reported annual survival rates and recruitment. These estimates are similar to reported estimates of lambda in other studies (Bridges 2005, Ryan 2009, Sawaya 2012). Bridges (2005), working within a shorter time period (1998–2001), reported a λ of 1.07 when both sexes were combined and acknowledged the need for long-term data sets when evaluating bear population dynamics. Brongo et al. (2005) further recognized that long-term studies of 10 years or more would yield a more reliable estimation of λ. Furthermore, Clark and Eastridge (2006) reported similar estimates of population growth using mark-recapture data in Pradel models and they were confident that mark-recapture techniques were an acceptable method of estimating λ. Our survival rates are similar to other studies (Hebblewhite et al. 2003, Brongo et al. 2005) as are the recruitment rates we report (Baldwin and Bender 2009). We believe both in situ recruitment of juvenile bears and immigration from the California portion of the Sierra Nevada black bear population contribute to the recruitment of bears into our study area and the resulting high estimates of λ. Given that parts of our study area may be acting as a population sink for black bears (Beckmann and Lackey 2008), immigration likely affects this population's resiliency. We could not, however, differentiate between juvenile recruitment and immigration.

Long-term studies of carnivores and more specifically black bears are uncommon because of the secretive nature of bears, the intensity of the effort required to capture and mark bears over an extended length of time, and the funding necessary for such projects (Pelton and van Manen 1996). Furthermore, short-term studies of these animals can produce results that would otherwise be interpreted differently (Brongo et al. 2005). We demonstrated that a sample of 197 marked bears over a 12-year study period was sufficient to estimate population size and life history parameters of a large carnivore population. This long-term effort allowed us to not only estimate population size with narrow confidence intervals but to estimate intrinsic rate of population increase (λ) as well as separate demographic estimates for males and females. Our estimated rate of increase ($\lambda = 1.16$) represents the mean rate of increase over the duration of the study and indicates that the black bear population in Nevada is increasing by about 16% per year. Similarly, the California Department of Fish and Game's published estimates of the state's bear population increased by about 15.7% during the same time period as our study (California Department of Fish and Game-Draft Environmental Document 2011). Although California's estimate is not a statistical estimate of λ, it is similar to our reported statistical estimate.

We have demonstrated that capture-recapture techniques are extremely valuable in enhancing our understanding of how humans and their activities affect carnivore populations (e.g., see Beckmann and Berger 2003*a*, Beckmann and Lackey 2008). The result of our long-term marking effort is documentation of an increasing black bear population.

MANAGEMENT IMPLICATIONS

Our use of historical records depicting presence of black bears in the interior of Nevada justifies the revision of historical range maps for black bears in North America. The extirpation of this species from the state's interior, due in part to landscape-level habitat changes associated with clear-cut logging illustrates the influence of forested habitat types on the perpetual existence of black bears in the Great Basin and possibly to the continued expansion of this species into historical habitat.

With increasing human–bear conflicts, management agencies have adjusted their policies and programs for dealing with these increases, and have tested and evaluated management options that are less costly and time consuming while upholding the public's expectations (Spencer et al. 2007). Spencer et al. (2007) identified several management options that agencies employ as a result of increasing conflicts between humans and black bears. In Nevada, where human–black bear conflicts are still a relatively new experience (Goodrich 1990, Beckmann and Berger 2003*a*), the need exists for reliable population estimates as this bear population expands. Additionally, as NDOW and the people of the state of Nevada make decisions on matters such as population management, non-lethal management options, and if black bear population expansion into former range is desirable, managers should have the proper perspective on historical, current, and expanding distributions of black bears.

Our data were used by the state of Nevada Board of Wildlife Commissioners in their 2010 decision to approve a legal hunting season for the first time in the state's history and their 2011 decision to make the hunt a permanent regulation. Until this time, NDOW did not have a population management option in place but relied on aversive conditioning of black bears and public education as the sole means of managing the state's increasing bear population (Lackey 2010).

Managers rarely have the opportunity to conduct long-term research on large carnivores. However, we have demonstrated that these long-term studies combined with intense mark-recapture efforts can provide managers with the data necessary to make decisions based on rigorous science, especially when those decisions can be polarizing, as is often the case with charismatic megafauna such as black bears. We emphasize that mark-recapture monitoring of this population should continue; we continue to investigate the role of immigration from the California portion of this population and how this facet of recruitment is affecting the population growth rate. The rate at which this population is expanding into historical habitat is a variable still unknown at this time and land use agencies and NDOW should consider this factor when evaluating management goals.

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APPENDIX A. SAMPLE HISTORICAL REFERENCES FOR BLACK BEARS

1. Clark, Bennett C.—Diary of a Journey from Missouri to California in 1849. Edited by Ralph P. Bieber and found in the Missouri Historical Review, Volume XXIII, Number 1, October, 1923, pp. 3–43. [Huntington F461 M6]
   July 29, 1849— . . . *"We learned today from an ox-train that 4 bear attacked & killed a cow belonging to them yesterday in open daylight. There is more game along here than we have seen since we left Bear River—Large rabbits, deer, bear, & water foul"* (sic). [Above the Humboldt Sink]
2. May 31, 1866—Territorial Enterprise (Virginia City) A strange animal—what is it?—*Yesterday . . . captured a small animal on the side of Mount Davidson, and brought him to town . . . It is apparently young and of the fox, wolf, or coyote species, having stiff ears, a long nose, and is of a dark brown or cinnamon color. He is quite shaggy, and some pronounce it a cinnamon bear . . .*
3. September 11, 1875—Silver State (Winnemucca) From Cornucopia— . . . *Hunters are out almost every day killing the game in the country. Steve Frum was out the other day and came across a young black bear which he succeeded in killing, and brought it to town; it would weigh about sixty-five pounds. He sold it to D. Greyson, who dressed it and hung it at the shop [Butcher shop] . . .*
4. January 18, 1878—Eureka Sentinel A bear—*Louis Brandt informs us that a huge bear has been seen in Antelope Valley by the residents of that place, and still haunts that vicinity. Some of our hunters had better interview Bruin and bring him into town. It would be a good chance to display their skill and prowess.*
5. September 11, 1879—Territorial Enterprise (Virginia City). . . at present in the Sierras . . . Bear are also more abundant than they have been for several years.
6. August 3, 1880—Nevada Daily Tribune (Carson City) Bears at Tahoe—*It is said that bears were never so plentiful in the vicinity of Lake Tahoe as they are this year—in fact, "The woods are full of them." On Mrs. Crocker's place at Idlewild, a day or two since, the dogs treed a full grown cinnamon bear and the coachmen recently captured a cub on the place.*
7. January 6, 1922—Humboldt Star (Winnemucca) Kills large animals in Bruno Mountains—*James Bryant, trapper and hunter, well-known throughout this section, arrived in town Monday evening from the northern part of the county and Idaho . . . When in the Bruno Mountains, on the boundary of Nevada and Idaho, he shot three young bears and expects to have a coat made from the hides . . .*
8. February 8, 1930—Reese River Reveille (Austin) Nevada is leader in coyote catching— . . . *The predatory animal control bureau was established thirteen years ago and since that time . . . and six bears were killed in Nevada by government-state trappers.*
9. November 3, 1931—Elko Free Press Big game— . . . *seldom that bear are found in this vicinity. Now and then one is reported but there are few times when the actual proof is shown . . . [2] recently lassoed and strangled a black bear near Charleston . . . believed the animal came in from Idaho, McKnight saw two of them . . . Indeed the killing of a bear in this county has become such a rarity that it is considered a big story.*