Survival Rates of Cougars in Oregon From 1989 to 2011: A Retrospective Analysis

DARREN A. CLARK,1,2 Oregon Cooperative Fish and Wildlife Research Unit, Department of Fisheries and Wildlife, Oregon State University, Corvallis, OR 97331, USA
BRUCE K. JOHNSON, Oregon Department of Fish and Wildlife, 1401 Gekeler Lane, La Grande, OR 97850, USA
DEWAINE H. JACKSON, Oregon Department of Fish and Wildlife, 4192 North Umpqua Hwy, Roseburg, OR 97470, USA
MARK HENJUM,‡ Oregon Department of Fish and Wildlife, 107 20th Street, La Grande, OR 97850, USA
SCOTT L. FINDHOLT, Oregon Department of Fish and Wildlife, 1401 Gekeler Lane, La Grande, OR 97850, USA
JAMES J. AKENSON,3 Oregon Cooperative Fish and Wildlife Research Unit, Department of Fisheries and Wildlife, Oregon State University, Corvallis, OR 97331, USA
ROBERT G. ANTHONY,† Oregon Cooperative Fish and Wildlife Research Unit, Department of Fisheries and Wildlife, Oregon State University, Corvallis, OR 97331, USA

ABSTRACT Cougar (Puma concolor) management in Oregon is unique because hunting cougars with dogs was allowed through the 1994 hunting season, but thereafter Ballot Initiative Measure 18 prohibited the use of dogs to pursue cougars. Since 1995, hunting seasons have become increasingly longer with more tags sold. The effects of changing management structure on survival rates and causes of mortality of cougars are not well understood. We investigated survival and documented causes of mortality of radiocollared cougars at 3 study areas in Oregon from 1989 to 2011 under contrasting management strategies. The Catherine Creek (1989–1996) and Jackson Creek (1993–2002) studies overlapped the prohibition of hunting cougars with dogs, and the Wenaha, Sled Springs, and Mt. Emily (WSM) study was conducted from 2002 to 2011 when hunting cougars with dogs was illegal. Hunting mortality was the most common cause of death for sub-adult and adult cougars in Catherine Creek pre- (18 of 23 mortalities) and post-Measure 18 (1 of 2 mortalities) and WSM (24 of 53 mortalities) study areas in northeast Oregon. In contrast, natural mortality was the most common cause of death of sub-adults and adults at the Jackson Creek (25 of 38 mortalities) study area in southwest Oregon, but hunting mortality was most common prior to the passage of Measure 18 (3 of 3 mortalities). We estimated annual survival rates of cougars using known fate models in Program MARK. Annual survival rates of adult males were lowest at Catherine Creek prior to the passage of Measure 18 (\(S = 0.57; 95\% \text{ CI} = 0.39–0.73\)) and increased after Measure 18 (\(S = 0.86; 95\% \text{ CI} = 0.79–0.92\)), which were similar to those rates observed at Jackson Creek pre- and post-Measure 18 (\(S = 0.78; 95\% \text{ CI} = 0.65–0.88\)) and WSM (\(S = 0.82; 95\% \text{ CI} = 0.69–0.91\)). Regardless of hunting regulations, annual survival rates of adult females was similar among study areas (Catherine Creek pre- and post-Measure 18 [\(S = 0.86; 95\% \text{ CI} = 0.79–0.92\)]; Jackson Creek pre- and post-Measure 18 [\(S = 0.85; 95\% \text{ CI} = 0.77–0.91\)]; WSM [\(S = 0.85; 95\% \text{ CI} = 0.76–0.90\]). At Jackson Creek pre- and post-Measure 18 and WSM, sub-adult males (1–3 years) had significantly lower survival than sub-adult females, but survival rates of males and females were similar by age 4 or 5 years. At WSM, survival declined for both sexes at older ages (8–13 years), but this decline was not observed at Jackson Creek pre- or post-Measure 18. The effect of increasing age on cougar survival should be considered when using survival rates to estimate population growth rates. We did not detect an effect of age on cougar survival at the Catherine Creek study area pre- or post-Measure 18, which we attributed to selective harvest of prime-aged, male cougars prior to the passage of Measure 18 and lack of mortality post-Measure 18. Managers should understand local sources of mortality when setting harvest regulations because sources of mortality may vary widely within and among jurisdictions, even if management practices are similar. Because of low hunter success rates when hunting cougars without dogs, survival rates of cougars managed under this hunting regime should be substantially higher than areas where use of dogs is legal. This suggests the ability of managers to effectively manipulate survival rates of cougars to meet population management objectives will be dependent on available hunting methods. Published 2014. This article is a U.S. Government work and is in the public domain in the USA.

KEY WORDS cougar, hunting, mortality, mountain lion, Oregon, Puma concolor, pursuit dogs, survival rates.
In 1994, Ballot Initiative Measure 18 (hereafter Measure 18) was passed by Oregon voters that prohibited the use of dogs to either pursue or hunt cougars (*Puma concolor*) following the 1994 hunting season. In response to cougar populations increasing statewide post-Measure 18 (Kiester and Van Dyke 2002) and low success rates of hunting cougars without dogs (Oregon Department of Fish and Wildlife [ODFW] 2006), hunting seasons, harvest quotas, and bag limits for cougars have become increasingly liberal in Oregon (Table S1, available online at www.onlinelibrary.wiley.com). Immediately following Measure 18 (1995–1996), cougar harvest declined dramatically, which occurred because of limited opportunity (i.e., expensive and limited numbers of tags coupled with short hunting seasons using inefficient methods). As tag prices declined and season lengths increased, cougar harvest increased but leveled off in recent years (ODFW 2006, 2012). Because of the unique changes in hunting regulations in Oregon compared to most other western states and Canadian provinces (i.e., variation in the use of dogs to hunt cougars; Cooley et al. 2011), we were interested in estimating sources of mortality and survival rates of cougars before and after Measure 18, and comparing these estimates to other areas where cougars are hunted to determine if the prohibition of hunting cougars with dogs affected cougar survival.

Hunting regulations are likely to have the greatest effect on survival rates of cougars because harvest is the primary source of mortality in most cougar populations (Hornocker 1970, Logan et al. 1986, Lambert et al. 2006, Robinson et al. 2008). In hunted populations, female cougars tend to have higher survival rates than males (Lambert et al. 2006; Robinson et al. 2008; Cooley et al. 2009a, b), likely because males are selectively harvested when dogs are used to hunt cougars (Anderson and Lindzey 2005, Zornes et al. 2006). Sex-biased harvest is less common in areas where hunters are not allowed to use dogs to hunt cougars (Zornes et al. 2006), which could lower survival rates of females and increase those of males compared to populations where males are selectively harvested; however, information to support this prediction is lacking. Support for this prediction could have important implications for cougar management because population growth rates of cougars are most sensitive to changes in female survival (Lambert et al. 2006; Robinson et al. 2008; Cooley et al. 2009a, b).

Adult cougars have greater survival rates than kittens and sub-adults (Ross and Jalkotzy 1992, Beier and Barrett 1993, Logan and Sweanor 2001), but little is known about the effect of increasing age on adult survival. Effect of age on cougar survival has typically been estimated for age classes (e.g., juvenile, sub-adult, and adult). This approach assumes cougars have similar survival rates once they reach adulthood; however, natural mortality rates of most long-lived mammals are lowest at intermediate ages and increase at older ages (Caughley 1966). To our knowledge, estimates of age-specific survival have only been reported for a cougar population in the Greater Yellowstone Ecosystem where older individuals had lower survival rates than prime-aged adults (Ruth et al. 2011). Documenting age-specific effects on survival can allow managers to identify life-stages with high natural mortality rates or high harvest rates that need protection or those that may be able to withstand additional exploitation to reduce populations depending on management objectives. Furthermore, estimates of age-specific survival would increase the reliability of population models used to monitor local cougar populations because the model would more accurately reflect reality (Caswell 2001, Morris and Doak 2002).

Cougars have been radiocollared in Oregon since 1989, which provided an opportunity to conduct a retrospective analysis to assess causes of mortality and estimate cougar survival rates. Our objectives with this retrospective analysis were to 1) document sources of cougar mortality in Oregon across different management regimes and ecosystems, 2) estimate survival rates of cougars pre- and post-Measure 18, and 3) determine effects of age on cougar survival. We predicted legal harvest would be the primary cause of mortality at all study areas as seen in other hunted cougar populations (Hornocker 1970, Logan et al. 1986, Lambert et al. 2006, Robinson et al. 2008). We also predicted non-hunting, human-caused mortality would increase over time because statewide cougar populations have increased (Kiester and Van Dyke 2002, ODFW 2006) and human-cougar conflict usually increase as cougar populations increase (Beier 1991) and/or in response to changing attitudes and decreased tolerance of large carnivores over time (Wolch et al. 1997, Schwartz et al. 2003). In response to selective harvest of males when using dogs to hunt cougars (i.e., pre-Measure 18; ODFW 2006, Zornes et al. 2006) and non-selective harvest using opportunistic hunting strategies (i.e., post-Measure 18; ODFW 2006, Zornes et al. 2006), we predicted male survival would increase and female survival decrease post-Measure 18. Because of male-biased dispersal patterns, we predicted sub-adult males would have lower survival than adult males (Ross and Jalkotzy 1992, Beier and Barrett 1993, Logan and Sweanor 2001) regardless of hunting regulations. Finally, we predicted survival would increase with age, peak at prime-ages, and decline at older ages.

**STUDY AREA**

We investigated cougar survival and causes of mortality at 3 study areas in Oregon between 1989 and 2011 (Fig. 1). Cougars were radiocollared at the Catherine Creek Wildlife Management Unit (WMU; approx. 1,700 km²) from 1989 to 1996, the Jackson Creek study area (Dixon and Evans Creek WMUs; approx. 6,700 km²) from 1993 to 2002, and 3 contiguous WMUs in northeast Oregon (Wenaha, Sled Springs, and Mt. Emily; hereafter WSM; approx. 5,350 km²) from 2002 to 2011. The ability to hunt cougars with dogs varied over the time periods of the studies (Table 1). The Catherine Creek and Jackson Creek studies overlapped the prohibition of dogs to hunt cougars, which allowed us to directly test for an effect of this change in management on cougar survival after 1994. The post-Measure 18 portion of the Jackson Creek (1995–2002) study was conducted when cougar hunting seasons were limited to 4–7 months. In
contrast, the WSM study was conducted when hunting seasons had increased to 10–12 months.

Mule deer (*Odocoileus hemionus hemionus*), Rocky Mountain elk (*Cervus elaphus nelsoni*), and white-tailed deer (*O. virginianus*) were the primary prey species available to cougars at Catherine Creek and WSM. Black-tailed deer (*O. hemionus columbianus*) and Roosevelt elk (*C. elaphus roosevelti*) were the primary prey species available to cougars at Jackson Creek. Other large and medium-sized carnivores present within all study areas included black bear (*Ursus americanus*), coyote (*Canis latrans*), and bobcat (*Lynx rufus*). At the time of our studies, no wolf (*C. lupus*) packs were documented in any of the study areas. Vegetation patterns at study areas in northeast Oregon were strongly influenced by topography, elevation, and aspect. South-facing slopes were dominated by herbaceous vegetation and north-facing slopes were dominated by mixed-conifer stands (Franklin and Dynness 1973). Common tree species at Catherine Creek and WSM included ponderosa pine (*Pinus ponderosa*), Douglas-fir (*Pseudotsuga menziesii*), grand fir (*Abies grandis*), larch (*Larix occidentalis*), and lodgepole pine (*P. contorta*). In contrast, vegetation patterns at Jackson Creek were more homogenous, and most areas were either mixed-conifer or deciduous dominated forest stands (Franklin and

![Figure 1. Locations of study areas where survival rates and causes of mortality of cougars were estimated from 1989 to 2011 in Oregon, USA. The Catherine Creek study was conducted from 1989 to 1996, the Jackson Creek study was conducted from 1993 to 2002, and the Wenaha-Sled Springs-Mt. Emily study was conducted from 2002 to 2011.](image)

Table 1. Summary description of study areas in Oregon, USA where we monitored survival rates and sources of mortality of cougars from 1989 to 2011.

<table>
<thead>
<tr>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td>Use of dogs to hunt cougars</td>
<td>Primary mortality source</td>
<td>Yes</td>
<td>No</td>
<td>Yes</td>
<td>No</td>
<td>No</td>
</tr>
<tr>
<td>Females</td>
<td>Harvest</td>
<td>Natural</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Males</td>
<td>Harvest</td>
<td>NA</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Secondary mortality source</td>
<td>Females</td>
<td>Natural</td>
<td>Harvest</td>
<td>NA</td>
<td>Other*</td>
<td></td>
</tr>
<tr>
<td>Males</td>
<td>Other and natural</td>
<td>NA</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

* WSM = Wenaha, Sled Springs, and Mt. Emily Wildlife Management Units.
* Other sources of mortality include: vehicle killed, poaching, and trapping.
* Both sources of mortality were equal.
Dyreness 1973). Common tree species within the Jackson Creek study area included ponderosa pine, sugar pine (P. lambertiana), Douglas-fir, white fir (A. concolor), mountain hemlock (Tsuga mertensiana), Oregon white oak (Quercus garryana), California black oak (Q. kelloggii), and Pacific madrone (Arbutus menziesii).

METHODS

Cougar Capture and Monitoring

All cougar capture and handling procedures were outlined and approved by ODFW’s wildlife veterinary, the Starkey Experimental Forest and Range, Animal Care and Use Committee (IACUC No. 92-F-0004), and followed the guidelines of the American Society of Mammalogists for the use of wild mammals in research (Sikes and Gannon, 2011). Cougar capture was dependent upon suitable tracking conditions (i.e., recent snowfall) and restricted to winter months (Nov–Apr). Each winter over the course of our studies, we searched for recently made cougar tracks (i.e., within the past 24 hr) along roads within study areas. We did not selectively pursue cougars and dogs were allowed to follow tracks from any sub-adult or adult. Our sampling scheme should have resulted in a representative sample of cougars in areas with road access assuming behavior was not biased by sex or age class in avoidance of roads we used to locate tracks. Because of a lack of road access, cougars occupying wilderness areas were likely underrepresented in our sample. After being treed, we immobilized cougars with a mixture of Ketamine (200 mg/ml; Fort Dodge Animal Health, Fort Dodge, IA) and xylazine (20 mg/ml; Rompun®; Bayer, Inc., Shawnee Mission, KS) or medetomidine (20 mg/ml; Domitor®; Pfizer Animal Health, New York, NY) at a dosage of 0.4 ml per 10 kg of body mass, administered via remote injection from a dart gun. Upon immobilization, we weighed cougars and determined sex and age. We determined ages of cougars first captured, but not necessarily radiocollared, as kittens or sub-adults (1 yr; Catherine Creek = 22, Jackson Creek = 30, WSM = 20) using pelage spotting progression (Shaw 1986), weights (Laundré and Hernández 2002), or tooth wear (Ashman et al. 1983, Shaw 1986). Whenever possible, we extracted the first premolar of adult cougars (Catherine Creek = 34, Jackson Creek = 28, WSM = 47) to determine age from cementum annuli analysis (Trainer and Matson 1988). In the event we were unable to extract a premolar from adult cougars (Catherine Creek = 2, Jackson Creek = 21, WSM = 30), we obtained field estimates of cougar age using evidence from tooth wear (Ashman et al. 1983, Shaw 1986) or gum-line recession (Laundré et al. 2000). We marked sub-adult and adult cougars with a very high frequency (VHF; Telonics MOD-500 or MOD-600; Telonics, Inc., Mesa, AZ) or global positioning system (GPS; Lotek 4400S or Lotek 7000SA; Lotek Engineering, Newmarket, ON, Canada) radiocollar containing mortality sensors. We attached 2 permanent, numbered ear tags or tattooed 1 ear to uniquely identify each cougar. Prior to release, we administered yohimbine (0.125 mg/kg; Yobine®; Lloyd Laboratories, Shenandoah, IA) as an antagonist for xylazine.

We monitored fates of individual cougars via radiotelemetry signals from the ground and fixed-wing aircraft. Frequency of aerial surveys varied by study, but typically occurred at least once every month. During each survey, we recorded fates (live or dead) and approximate location of cougars. We were interested in estimating annual survival rates of cougars and attempted to confirm fates of individual cougars at the end of each calendar year. We recorded cougars not located during telemetry flights as missing. If we could not determine the fate of an individual at the end of the year and in subsequent flights, we right-censored the cougar from the analysis. If the mortality sensor indicated the cougar died, we located the carcass as soon as possible to determine cause of death. If cause of death could not be determined in the field, we submitted the cougar carcass for necropsy at the Veterinary Diagnostic Lab at Oregon State University, College of Veterinary Medicine (Corvallis, OR, USA) or United States Fish and Wildlife Service Forensic Laboratory (Ashland, OR, USA). Regulations required that harvested cougars be checked at a local ODFW office within 72 hours of harvest where the sex, age, approximate harvest location, and date of death were recorded.

Analysis

To investigate causes of mortality, we pooled cougar deaths into 3 classes: 1) hunter harvest, 2) non-hunting human-caused mortality (e.g., administrative removal, vehicle killed cougars, illegal harvest), and 3) natural mortality (e.g., disease, injury, cougar predation). We divided Catherine Creek and Jackson Creek into 2 time periods, pre- and post-Measure 18, to account for any changes in sources of mortality related to changes in management. Preliminary analysis using a Pearson’s Chi-square test (R Development Core Team 2011) indicated frequencies of each cause of mortality were similar between age classes (i.e., sub-adult and adult; Table S2, available online at www.onlinelibrary.wiley.com). Consequently, we pooled data at each study area for each management system (i.e., pre- vs. post-Measure 18) to increase sample sizes and reduce Type II errors (Zar 1999). We censored individuals that died of unknown causes from this analysis. We examined frequencies of mortality causes between study areas and management system separately for each sex using a Pearson’s Chi-square test (R Development Core Team 2011), and determined significance using an alpha of 0.05.

We estimated annual survival rates (S) of cougars in Program MARK using known-fate models for radiocollared individuals (White and Burnham 1999). We used a modified Kaplan and Meier (1958) estimator that allowed for staggered data entry and censoring of individuals (Pollock et al. 1989). We used Akaike’s Information Criterion corrected for small sample sizes (AICc) to rank candidate models (Burnham and Anderson 2002). We used the difference between AICc of the best model and the ith model (ΔAICc) to identify closely competing models (ΔAICc ≤ 2.0; Burnham and Anderson 2002). We used Akaike weights to
evaluate the relative support for each candidate model (Burnham and Anderson 2002). To determine significance of the effect of various factors in the model, we evaluated whether regression coefficients (β) and their associated 95% confidence interval overlapped 0 according to the methods described by Anthony et al. (2006). Our primary interest with this analysis was to determine the effect of age on survival of cougars, so we used the best model that included an effect of age to estimate survival rates of cougars at each study area.

We determined fates of individual cougars annually. We included individuals in the dataset each year they were radio-collared and censored them during any year where we did not monitor them the entire calendar year. We conducted a separate survival analysis for each study area because minimal overlap existed in timing of each study. We developed a set of candidate models based on biologically plausible hypotheses to test for differences in survival among sex, age, and time. We used previously outlined approaches when building and naming our candidate model set (Lebreton et al. 1992, White and Burnham 1999). We tested for differences in survival rates between sexes because previous studies have indicated females have higher survival than males (Logan and Sweanor 2001, Lambert et al. 2006, Robinson et al. 2008). We investigated models that incorporated 5 temporal effects on cougar survival including constant (.), time varying (t), linear (T), log-linear (lnT), and quadratic (TT) trends. We tested for these temporal effects because they would account for any undocumented temporal or environmental variation that may influence cougar survival. We modeled additive (+) and interactive (×) combinations of sex and time when appropriate. For example, if the linear trend (T) model ranked higher than the constant survival (.) model, we modeled the linear trend as an interactive and additive effect with sex. We also investigated 2 temporal models that directly tested for an effect of changes in management (i.e., pre- versus post-Measure 18) on survival rates at the Catherine Creek and Jackson Creek study areas. Harvest of cougars with the use of dogs was male biased compared to harvest without the use of dogs (ODFW 2006, Zornes et al. 2006), so we included a model that indicated female survival would be constant pre- and post-Measure 18, but male survival would differ. We also included a model that indicated male and female survival would increase post-Measure 18.

We determined ages of individual cougars at either time of capture or death and we extrapolated ages in subsequent or previous years from this point. We treated age as a continuous, age-specific covariate and considered 3 separate functional relationships to evaluate an effect of age on cougar survival: linear (Age), log-linear (lnAge), and quadratic (Age^2) and considered additive (+) and interactive (×) relationships between sex and age. The linear and log-linear trends in age-specific survival would identify effect of increasing age on cougar survival, and a quadratic model would also account for effect of old age, if any, on survival. We modeled age as constant effect over time but allowed ages of individual cougars to change each year. Where age was not determined for a cougar (n = 1 at Catherine Creek; n = 1 at Jackson Creek), we assigned the individual an age that was equal to the mean age of radio-collared cougars during the year they were first captured. This should have minimal effects on results because the mean of the observed covariate values will not change (i.e., the estimated effect is the same) but the variance will be slightly smaller (Cooch and White 2013).

We used the best model that included effect of age (yrs) to generate point estimates of sub-adult (1 yr) and mean adult (≥2 yr) survival to compare to published literature. We calculated mean age of adult cougars using a weighted mean

---

Figure 2. Distribution of the proportion of encounter histories, sorted by age and sex, used to estimate survival of cougars at the (a) Catherine Creek (1989–1996), (b) Jackson Creek (1993–2002), and (c) Wenaha-Sled Springs-Mt. Emily (2002–2011) study areas in Oregon. We included 147, 223, and 247 year and age-specific encounter occasions in the analysis of survival at Catherine Creek, Jackson Creek, and Wenaha-Sled Springs-Mt. Emily study areas, respectively.
where the weighting factor was the number of encounter occasions (Fig. 2) that we monitored individuals of a particular sex and age at each study area (yr; Catherine Creek: male = 4.3 [n = 28, SE = 1.5], female = 4.8 [n = 83, SE = 0.7]; Jackson Creek: male = 5.7 [n = 81, SE = 0.9], female = 5.4 [n = 119, SE = 0.9]; WSM: male = 6.0 [n = 92, SE = 0.4], female = 4.9 [n = 163, SE = 0.3]). After determining the mean age of cougars at each study area, we used this value in the best survival model to generate mean survival rates of adult cougars.

RESULTS

We radiocollared 58 cougars (male = 21, female = 37) at Catherine Creek, 79 cougars at Jackson Creek (male = 37, female = 42), and 97 cougars (male = 40, female = 57) at WSM in our analysis of survival. Some cougars were monitored multiple years and we monitored a mean of 19 (range = 9–26; Table S3, available online at www.onlinelibrary.wiley.com), 22 (range = 9–35; Table S4, available online at www.onlinelibrary.wiley.com), and 25 (range = 15–31; Table S5, available online at www.onlinelibrary.wiley.com) cougars annually at Catherine Creek, Jackson Creek, and WSM, respectively. At Catherine Creek and Jackson Creek study areas, sub-adults (1-yr-old) were most frequently monitored (Fig. 2a and b). In contrast, 4-year-old cougars were most frequently monitored at WSM (Fig. 2c). This may indicate our sample of cougars at WSM was not representative of the population (i.e., sub-adults were under sampled), which should have minimal effects on age-specific survival estimates so long as sampled individuals were representative of their age class; however, reduced sample sizes for individual ages will increase sample variance. During our study we lost radio-contact with 2 cougars at Catherine Creek, 7 cougars at Jackson Creek, and 6 cougars at WSM and we right-censored these individuals from our analysis. To the best of our knowledge, this censoring protocol was independent of cougar fates and did not result in positively biased survival estimates.

Frequency of hunting, natural, and non-hunting, human-caused mortality varied among study areas and according to management practices (i.e., pre- vs. post-Measure 18) for both males ([χ² = 26.34, P = 0.001; Fig. 3a]) and females ([χ² = 19.05, P = 0.01; Fig. 3b]). Hunting mortality was extremely limited at Jackson Creek, but was the only source of mortality-documented pre-Measure 18 (Fig. 3). Hunter harvest was also the primary source of mortality at Catherine Creek pre- and post-Measure 18 and at WSM. Natural mortalities occurred much more frequently at Jackson Creek following Measure 18 than were observed prior to Measure 18 and at WSM and Catherine Creek pre- or post-Measure 18 (Fig. 3). Natural mortalities at Jackson Creek were associated with disease or parasites (n = 15), cougar predation (n = 6), injuries (n = 3), and unknown natural causes (n = 1). Natural mortalities at Catherine Creek were associated with injuries (n = 2), cougar predation (n = 2), and unknown natural causes (n = 1). At WSM causes of natural mortalities included unknown natural causes (n = 7), disease or parasites (n = 2), injury (n = 2), and cougar predation (n = 1). Frequency of non-hunting, human-caused mortality was lowest at Catherine Creek and greatest at WSM (Fig. 3).

We used the best-ranked model to estimate cougar survival at the Catherine Creek study area, but 2 models had a ΔAIC < 2.0 and were considered competing with the best model (Table 2). The second-ranked model included effects of sex and a linear temporal trend on survival rates, but the coefficient for the linear temporal trend overlapped 0 (β = 0.17, 95% CI = −0.04 to 0.38) and we did not consider this model further. The third-ranked model indicated an effect of sex on survival rates, but did not include any effects of changes in management (i.e., pre- vs. post-Measure 18), which was an important effect in the best-ranked model (β = −1.58, 95% CI = −2.48 to −0.69). Consequently, we used the best ranked model (Table 2) for interpretation of results and this model reflected that survival was independent
of age, survival of males pre-Measure 18 ($\hat{S} = 0.57$, 95% CI = 0.39–0.73) was lower than post-Measure 18 ($\hat{S} = 0.86$, 95% CI = 0.79–0.92) and female survival was identical pre- and post-Measure 18 ($\hat{S} = 0.86$, 95% CI = 0.79–0.92). No evidence for an effect of age existed on cougar survival (Fig. 4a), because the best model including age had a $\Delta$AIC > 2.0 (Table 2), and the coefficient for age was centered near and overlapped 0 ($\hat{\beta} = -0.01$, 95% CI = -0.17 to 0.14).

The best model at Jackson Creek included an effect of sex on survival rates (Table 3), where females had higher survival than males ($\hat{\beta} = 0.92$, 95% CI = 0.25–1.59). All models that had a $\Delta$AIC < 2.0 included an effect of age on survival and these models accounted for 0.78 of the model weights (Table 3), which provided some support for an effect of age on survival. Furthermore, our primary objective was to estimate age-specific survival rates of cougars, so we used the best model that included an effect of sex and age ($\delta$Sex $\times$ lnAge; Table 3) to estimate age-specific survival rates of cougars. This model indicated survival varied by age (yrs) with female survival declining slightly with increasing age and male survival increasing with age, but female survival was higher than male survival at younger ages (Fig. 4b). The effect of age was not strongly supported because the coefficient for lnAge ($\hat{\beta} = 0.52$, 95% CI = -0.05 to 1.08) and the interaction between sex and lnAge ($\hat{\beta} = -0.69$, 95% CI = -1.53 to 0.14) were centered away from but overlapped 0. We found no evidence that survival was influenced by hunting regulations because models that included this effect had a $\Delta$AIC ≥ 3.8 (Table 3).

Our best model for survival at WSM included interactive effects between sex and age (Table 4). One model ($\delta$Sex $+$ Age) was considered competing with the best model, but this model was identical to the best model except it did not include an interactive effect between sex and age. In our best-ranked model, some of the coefficients for the effect of age (female $\hat{\beta} = 0.84$, 95% CI = 0.13–1.55, male $\hat{\beta} = -0.79$, 95% CI = -1.70 to 0.13) and age (female $\hat{\beta} = -0.07$, 95% CI = -0.13 to -0.01, male $\hat{\beta} = 0.05$, 95% CI = -0.03 to 0.12) overlapped 0; however, including effect of age substantially improved model fit, which indicated the interactive effect of sex and age explained some variation in cougar survival and we used our best-ranked model for interpretation of results (Table 4). Our best-ranked model indicated cougar survival followed a quadratic trend with age, and the relationship differed for males and females. Females had higher survival than males at younger ages, but males had similar survival by 4–6 years, and survival declined at older ages for both sexes (Fig. 4c).

**DISCUSSION**

**Causes of Mortalities**

With the exception of Jackson Creek following the passage of Measure 18, legal harvest was the greatest cause of mortality of radio-collared cougars, and harvest was also the greatest cause of mortality in other hunted cougar populations (Hornocker 1970, Logan et al. 1986, Lambert et al. 2006, Robinson et al. 2008). Hunting cougars with dogs greatly increased mortality of male cougars where male harvest was more than 2 times greater compared to when hunting with dogs was prohibited (Fig. 3). This was expected because hunting with dogs is more effective harvest method than hunting without dogs and can allow hunters to identify the sex of treed cougars and selectively harvest males, which may be considered trophy animals (Anderson and Lindzey 2005, Zornes et al. 2006). Harvest mortality of females was relatively consistent across studies, which was likely a consequence of avoidance of females by hunters pre-Measure 18 and non-selective, inefficient harvest post-Measure 18 (ODFW 2006, 2012). We attributed lower harvest rates of all cougars at Jackson Creek after passage of
Measure 18 compared to WSM to differences in habitat. Dense, contiguous forest cover is the dominant vegetative cover in southwest Oregon, and vegetative cover in northeast Oregon is strongly influenced by topography, elevation, and aspect, with substantially more open land cover (Franklin and Dyrness 1973). The increased visibility afforded hunters in northeast Oregon likely allowed hunters to more effectively locate and harvest cougars compared to southwest Oregon. Additionally, we speculate higher harvest rates at WSM compared to Jackson Creek post-Measure 18 could be related to refinements in hunting methods (i.e., predator calling, snow tracking) that may increase harvest rates without the use of dogs or increased tag sales and season lengths that resulted in greater hunter effort over time.

The relatively high levels of natural mortality at Jackson Creek following the passage of Measure 18 were unexpected because natural mortality has been documented as the primary cause of mortality only in unhunted cougar

![Figure 4](image-url)

Figure 4. Sex- and age-specific survival (S) estimates and 95% confidence intervals of cougars at (a) Catherine Creek (1989–1996), (b) Jackson Creek (1993–2002), and (c) Wenaha-Sled Springs-Mt. Emily study areas in Oregon, USA (1993–2011). We generated estimates using the model S(Female(.)) = MalePost(.) + MalePre(.)) for Catherine Creek, $S(\text{sex} \times \text{lnAge})$ for Jackson Creek, and $S(\text{Sex} \times \text{Age}^2)$ for Wenaha-Sled-Mt. Emily study areas, respectively. The displayed estimate of age-specific survival for male cougars at Catherine Creek represent survival rates prior to the passage of Measure 18 (MalePre; 1989–1994), and survival rates following Measure 18 (MalePost; 1995–1996) were identical to females.

Table 3. Model selection results for cougar survival (S) at the Jackson Creek study area in southwest Oregon, USA (1993–2002). Models are ranked according to Akaikes Information Criterion corrected for small sample sizes (AICc).

<table>
<thead>
<tr>
<th>Model</th>
<th>AICc</th>
<th>ΔAICc</th>
<th>$w^b_0$</th>
<th>Likelihood</th>
<th>Kc</th>
</tr>
</thead>
<tbody>
<tr>
<td>S(Sex)</td>
<td>218.72</td>
<td>0.00</td>
<td>0.20</td>
<td>1.00</td>
<td>2</td>
</tr>
<tr>
<td>S(Sex × lnAge)</td>
<td>219.11</td>
<td>0.39</td>
<td>0.16</td>
<td>0.82</td>
<td>4</td>
</tr>
<tr>
<td>S(Sex + Age2)</td>
<td>219.23</td>
<td>0.51</td>
<td>0.16</td>
<td>0.77</td>
<td>4</td>
</tr>
<tr>
<td>S(Sex + lnAge)</td>
<td>219.74</td>
<td>1.02</td>
<td>0.12</td>
<td>0.60</td>
<td>3</td>
</tr>
<tr>
<td>S(Sex + Age)</td>
<td>220.00</td>
<td>1.28</td>
<td>0.11</td>
<td>0.53</td>
<td>4</td>
</tr>
<tr>
<td>S(Sex + Age2)</td>
<td>220.03</td>
<td>1.32</td>
<td>0.10</td>
<td>0.52</td>
<td>6</td>
</tr>
<tr>
<td>S(Sex + Age)</td>
<td>220.67</td>
<td>1.95</td>
<td>0.08</td>
<td>0.38</td>
<td>3</td>
</tr>
<tr>
<td>S(Sex + Pre(.)) ≠ Post(.)</td>
<td>222.58</td>
<td>3.87</td>
<td>0.03</td>
<td>0.14</td>
<td>4</td>
</tr>
<tr>
<td>S(.)</td>
<td>223.96</td>
<td>5.24</td>
<td>0.01</td>
<td>0.07</td>
<td>1</td>
</tr>
<tr>
<td>S(T)</td>
<td>224.67</td>
<td>5.95</td>
<td>0.01</td>
<td>0.05</td>
<td>2</td>
</tr>
<tr>
<td>S(lnT)</td>
<td>225.09</td>
<td>6.38</td>
<td>0.01</td>
<td>0.04</td>
<td>2</td>
</tr>
<tr>
<td>S(MalePre(.)) = MalePost(.))</td>
<td>225.36</td>
<td>6.64</td>
<td>0.00</td>
<td>0.02</td>
<td>2</td>
</tr>
<tr>
<td>S(TT)</td>
<td>226.17</td>
<td>7.45</td>
<td>0.00</td>
<td>0.02</td>
<td>3</td>
</tr>
<tr>
<td>S(t)</td>
<td>235.27</td>
<td>16.55</td>
<td>0.00</td>
<td>0.00</td>
<td>10</td>
</tr>
<tr>
<td>S(Sex × t)</td>
<td>239.54</td>
<td>20.82</td>
<td>0.00</td>
<td>0.00</td>
<td>20</td>
</tr>
</tbody>
</table>

* Pre refers to the time period when hunting cougars with dogs was legal;
Post refers to the time period when hunting cougars with dogs was illegal;
T is a linear time trend; TT is a quadratic time trend; t allows rates to differ among years; and (.) is constant survival.
$^b$ Akaike weight.
$^c$ No. of parameters in model.

Table 4. Model selection results for cougar survival (S) at the Wenaha, Sled Springs, and Mt. Emily study areas in northeast Oregon, USA (2002–2011). Models are ranked according to Akaikes Information Criterion corrected for small sample sizes (AICc).

<table>
<thead>
<tr>
<th>Model</th>
<th>AICc</th>
<th>ΔAICc</th>
<th>$w^b_0$</th>
<th>Likelihood</th>
<th>Kc</th>
</tr>
</thead>
<tbody>
<tr>
<td>S(Sex × Age2)</td>
<td>250.03</td>
<td>0.00</td>
<td>0.48</td>
<td>1.00</td>
<td>6</td>
</tr>
<tr>
<td>S(Sex × lnAge)</td>
<td>251.43</td>
<td>1.40</td>
<td>0.24</td>
<td>0.50</td>
<td>4</td>
</tr>
<tr>
<td>S(Sex × Age)</td>
<td>252.93</td>
<td>2.89</td>
<td>0.11</td>
<td>0.24</td>
<td>4</td>
</tr>
<tr>
<td>S(Sex × lnAge)</td>
<td>253.81</td>
<td>3.77</td>
<td>0.07</td>
<td>0.15</td>
<td>4</td>
</tr>
<tr>
<td>S(Sex + Age2)</td>
<td>254.15</td>
<td>4.12</td>
<td>0.06</td>
<td>0.13</td>
<td>3</td>
</tr>
<tr>
<td>S(Sex + lnAge)</td>
<td>256.90</td>
<td>6.87</td>
<td>0.02</td>
<td>0.03</td>
<td>3</td>
</tr>
<tr>
<td>S(Sex)</td>
<td>257.93</td>
<td>7.89</td>
<td>0.01</td>
<td>0.02</td>
<td>2</td>
</tr>
<tr>
<td>S(.)</td>
<td>258.87</td>
<td>8.84</td>
<td>0.01</td>
<td>0.01</td>
<td>1</td>
</tr>
<tr>
<td>S(TT)</td>
<td>260.24</td>
<td>10.21</td>
<td>0.00</td>
<td>0.01</td>
<td>3</td>
</tr>
<tr>
<td>S(lnT)</td>
<td>260.68</td>
<td>10.65</td>
<td>0.00</td>
<td>0.00</td>
<td>2</td>
</tr>
<tr>
<td>S(T)</td>
<td>260.91</td>
<td>10.87</td>
<td>0.00</td>
<td>0.00</td>
<td>2</td>
</tr>
<tr>
<td>S(t)</td>
<td>273.37</td>
<td>23.34</td>
<td>0.00</td>
<td>0.00</td>
<td>10</td>
</tr>
<tr>
<td>S(Sex × t)</td>
<td>289.14</td>
<td>39.11</td>
<td>0.00</td>
<td>0.00</td>
<td>20</td>
</tr>
</tbody>
</table>

* T is a linear time trend; TT is a quadratic time trend; t allows rates to differ among years; and (.) is constant survival.
$^b$ Akaike weight.
$^c$ No. of parameters in model.
populations, where intraspecific strife and aggression was the primary cause of mortality (Hemker et al. 1984, Beier and Barrett 1993, Logan and Sweanor 2001). Surprisingly, intraspecific strife and aggression was not the most common cause of natural mortality at Jackson Creek, except for subadult males (3 of 6 mortalities). Although we were unable to determine the exact cause of death for most natural mortalities ($n = 12$; 48%) in Jackson Creek, most cougars dying of identified natural causes ($n = 11$) were infected with a stomach nematode (*Cylicospirura* spp.). These nematodes cause intestinal lesions and parasite load ranged from minimal to extreme (1–562 worms/ cougar; Ferguson et al. 2011). The clinical effect of *Cylicospirura* was undetermined; however, extreme levels of infestation may reduce fitness of cougars by negatively affecting their ability to hunt large prey (Ferguson et al. 2011). The life history of this nematode is not well known, but because cougars are obligate carnivores, we speculate the parasite is transmitted via prey to predator. Few cougars were infected with *Cylicospirura* in WSM, and no infections were documented during the Catherine Creek study or in 39 necropsied cougars harvested in northeast Oregon from 1976 to 1978 (Rausch et al. 1983). These findings indicate this parasite and possibly the host may be relatively new to cougar populations in Oregon.

Human-cougar conflicts typically increase as cougar populations or development within cougar habitat increase (Beier 1991). Based on population reconstruction estimates (ODFW, unpublished data), cougar populations in our study areas have remained relatively stable since the late 1980s. Alternatively, attitudes toward large predators change over time (Wolch et al. 1997, Schwartz et al. 2003), and we speculate increased non-hunting, human-caused mortality observed at WSM was associated with a decreased tolerance of cougars by humans. Increased development in rural areas, which may increase encounter rates between cougars, humans, and livestock, is an additional explanation for increased non-hunting, human-caused mortality. Cougars monitored during our studies primarily occupied wildlands (i.e., national forest or industrial timber lands), and rarely used areas near human development. Therefore, increased human development likely did not contribute to increased non-hunting, human-caused mortality during our studies.

**Survival**

Male survival prior to Measure 18 at Catherine Creek ($\hat{S} = 0.57$) was at the upper range of values reported in other areas where hunting cougars with dogs was legal (Table S6, available online at www.onlinelibrary.wiley.com). Hunting opportunity during the Catherine Creek study was conservative (10 tags issued annually), season lengths short (1–31 Dec), and access limited. The study area was adjacent to the Eagle Cap Wilderness further reducing vehicle and hunter access. This limited hunting opportunity and access was much lower than observed in other areas where hunting cougars with dogs was legal (Table S6, available online at www.onlinelibrary.wiley.com) and likely explains why male cougars at Catherine Creek pre-Measure 18 had higher survival rates than previously reported in other populations. Therefore, the degree to which male survival is reduced in areas where hunting with dogs is legal should be dependent on the number of tags issued, access, and season lengths. Our estimates of adult male survival under an opportunistic (i.e., without dogs) hunting regime ($\hat{S} = 0.78–0.86$) were substantially higher than reported in populations where hunting with dogs was allowed but lower than other unhunted populations (Table S6, available online at www.onlinelibrary.wiley.com). We contend the inefficient (approx. 1–2% hunter success rates; ODFW 2012) and non-selective nature of cougar harvest without the use of dogs (ODFW 2006, Zornes et al. 2006) and more effective, male-biased harvest in areas where hunting with dogs is legal (Anderson and Lindzey 2005, Zornes et al. 2006) explained why survival rates of male cougars in our studies was greater than in areas where cougars are hunted with dogs (Table S6, available online at www.onlinelibrary.wiley.com).

Despite increased hunting opportunity (i.e., tags and season lengths) post-Measure 18, hunter success rates were sufficiently low (1–2% annually; ODFW, unpublished data) that harvest rates (Fig. 3b) and survival rates (Fig. 4; Table S6, available online at www.onlinelibrary.wiley.com) of females, regardless of age, did not differ across our studies. Survival rates of adult female cougars in our study areas (0.84–0.86) were greater than those observed in hunted populations in Utah, Montana, Arizona, and Washington (Table S6, available online at www.onlinelibrary.wiley.com) where hunting cougars with dogs was legal, and similar to those reported for females in an unhunted population in New Mexico (Table S6, available online at www.onlinelibrary.wiley.com). These comparisons indicated the effect of harvest on survival rates of female cougars is dependent on hunting method and intensity as regulated by quota or permit systems. For example, the level of female harvest mortality at our studies when the use of dogs was legal (0.09) and illegal (0.01–0.09) was lower than other hunted populations (e.g., 0.15; Robinson et al. 2008, 0.16; Cooley et al. 2009) where tag numbers and hunter success rates was sufficiently high to negatively affect female survival.

Quigley and Hornocker (2010:66) suggested “the inverse relationship between human-caused and natural mortality suggests a compensatory mechanism in which human-caused mortality is replacing natural mortality in human-impacted ecosystems.” We observed high levels of natural mortality in conjunction with low harvest rates at Jackson Creek post-Measure 18, and despite higher levels of human-caused mortality at other study areas (Fig. 3), overall survival rates were relatively consistent across studies (Table S6, available online at www.onlinelibrary.wiley.com). Although our study was not designed to assess the additive or compensatory nature of human-caused mortality on cougar survival, we agree with Quigley and Hornocker (2010) that human-caused mortality was partially compensatory, at least at low levels of human-caused mortality. We also agree with Cooley et al. (2009) that harvest mortality can be additive in heavily hunted populations and survival rates of adult males in...
Lower survival rates of sub-adult males compared to sub-adult females is a common occurrence in cougar populations (Anderson et al. 1992, Logan and Sweanor 2001, Lambert et al. 2006). Our results substantiated females have greater survival rates than males at younger ages (1–3 yr), and male-biased dispersal in cougars (Sweanor et al. 2000, Logan and Sweanor 2001, Thompson and Jenks 2010) likely explains the difference in survival between males and females at younger ages. By the time most males establish a territory (3–4 yrs; Logan and Sweanor 2001) survival rates of males at Jackson Creek and WSM were similar to females, which supported the conclusion that lower survival rates of males at younger ages are attributable to increased mortality factors encountered during dispersal. We documented a pattern of decreasing survival for both sexes of cougars at older ages at WSM, but surprisingly, this pattern was not observed at Jackson Creek. We conducted a post hoc analysis where we pooled data from Jackson Creek and WSM to estimate effect of age on cougar survival. The best model from this analysis was \( \hat{S}(\text{Sex} \times \text{Age}^2) \), and results were similar to those observed at WSM (Fig. 4c). As a result, we concluded our sample size was inadequate to estimate effect of old age on survival at the Jackson Creek study area. Ruth et al. (2011) also observed declining survival at older ages in a cougar population in Yellowstone’s northern range. Similar to cougar populations in Jackson Creek post-Measure 18 and WSM (Fi. 3), mortality attributable to hunter harvest was limited in Yellowstone’s northern range (Ruth et al. 2011). Consequently, declines in survival with increasing age may only be present in lightly hunted populations where a greater number of cougars survive to older ages. Not accounting for an effect of age-specific survival could have important implications for managers if survival rates are used to parameterize models to estimate population growth rates and size. In cases where older adults have lower survival, treating adults in an identical manner will cause survival rates of individuals with higher reproductive values to be lower than expected (i.e., older individuals will reduce the mean survival rate), which will contribute to conservative estimates of population growth (Morris and Doak 2002). Because acquiring a sufficient sample of individuals to estimate age-specific survival may be logistically or financially challenging, estimating survival for multiple age classes (e.g., Robinson et al. 2008) may provide the best alternative.

We did not to observe any effect of age on cougar survival at Catherine Creek, but male cougars in this study area were subjected to higher harvest levels than Jackson Creek and WSM. Mean age of all male cougars harvested at Catherine Creek was 5.7 years pre-Measure 18 \((n = 10; 1989–1994)\) and 3.9 years post-Measure 18 \((n = 46; 1995–2011)\), which suggested hunters using dogs disproportionately harvested older males (ODFW, unpublished data). Selective hunting pressure reduced survival rates of adult male cougars at Catherine Creek, causing their survival rates to be similar to sub-adults. This type of selective harvest may eliminate effect of age on survival in other hunted populations where prime-age individuals are selectively harvested. Additionally, our sample of radiocollared cougars was smallest at Catherine Creek and we may have lacked a sufficient sample to estimate age-specific survival rates.

**MANAGEMENT IMPLICATIONS**

Our results suggest opportunistic hunting of cougars (i.e., without dogs) can provide high levels of recreation while maintaining high survival rates of cougars because of the low success rates of hunters using this method. In systems where hunting cougars with dogs is illegal, managers may have difficulty using hunter harvest when they need to reduce populations to meet management objectives. Our results also indicated hunting of cougars with dogs can maintain high survival rates of female cougars, under conservative hunting levels (i.e., limited tag numbers), which may be compatible with maintaining cougar populations. However, managers must clearly define population objectives for cougars when providing hunting opportunities with dogs because excessive harvest can result in additive mortality (Cooley et al. 2009b) and population declines (Lambert et al. 2006). Background levels of natural mortality are effectively impossible to detect without intensive radiocollaring programs, which are not cost effective or logistically feasible across large spatial extents. Consequently, we recommend managers monitor population health and age structure through mandatory checks of harvested animal for diseases and parasites.

**ACKNOWLEDGMENTS**

Funding for the Catherine Creek study was provided by the ODFW. The Jackson Creek and Wenaha-Sled Springs-Mt. Emily studies were funded by the ODFW through the Federal Aid in Wildlife Restoration Grants W-89-R, W-90-R, and W-98-R. Additional funding was provided by the Oregon Hunters Association, Confederated Tribes of the Umatilla Indian Reservation, Rocky Mountain Elk Foundation, Blue Mountain Elk Initiative, and Blue Mountains Habitat Restoration Council. A portion of the study was conducted under the auspices of the Oregon Cooperative Fish and Wildlife Research Unit, with ODFW, Oregon State University, and U.S. Geological Survey cooperating while the lead author was a graduate student at Oregon State University. A draft of this manuscript was included in the lead author’s dissertation at Oregon State University. We are indebted to T. Bernot, L. Brown, T. Craddock, W. Craddock, G. Culver, L. East, K. Fomey, J. Howell, D. Johnson, S. Jones, and T. O’Leary for the training and skill of their dogs we used to capture cougars. Numerous individuals from the ODFW provided logistical support, procured funding, and helped capture and monitor cougars including J. Cadwell, P. Coe, V. Coggins, G. Davidson, L. Erickson, M. Hansen, H. Hayden, D. Jones, C. Nowak, J. Noyes, J. Orr, J. Paustian, A. Polanz, B. Ratliff, L. Robertson, J.

**LITERATURE CITED**


**LITERATURE CITED**


**LITERATURE CITED**


**LITERATURE CITED**


Associate Editor: John Squires.

SUPPORTING INFORMATION
Additional supporting information may be found in the online version of this article at the publisher’s web-site.