



Research Article

Using DNA to Describe and Quantify Interspecific Killing of Fishers in California

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ABSTRACT Interspecific killing is common among carnivores and can have population-level effects on imperiled species. The fisher (*Pekania [Martes] pennanti*) is a rare forest carnivore in western North America and a candidate for listing under the United States Endangered Species Act. Interspecific killing and intraguild predation are poorly understood in fishers and potential threats to existing western populations. We studied the prevalence and patterns of interspecific killing of fishers in the southern Sierra Nevada and Coastal Range of California. We collected forensic evidence and samples from the carcasses and predation sites, conducted full necropsies when possible, and used molecular methods to determine species of predators responsible for killing fishers. We recovered 101 (59 female, 42 male) fisher carcasses; for 62 (61%) carcasses, we attributed cause of death to interspecific killing. We found that bobcats (*Lynx rufus*, $n = 25$ fisher mortalities), mountain lions (*Puma concolor*, $n = 20$), and coyotes (*Canis latrans*, $n = 4$) were predators of fishers in our study areas. Bobcats killed only female fishers, whereas mountain lions more frequently killed male than female fishers, confirming our hypothesis that female fishers would suffer lethal attacks by smaller predators than would male fishers. Coyotes rarely killed fishers. We found differences in pathologic characteristics of the predation events among the 3 predator species, which may be helpful in identifying predator species. © 2014 The Wildlife Society.

KEY WORDS bobcat, *Canis latrans*, coyote, fisher, interspecific killing, intraguild predation, *Lynx rufus*, *Martes pennanti*, mountain lion, *Pekania pennanti*, predator, *Puma concolor*.

Interspecific killing is common in wildlife communities, often documented among the larger carnivorous mammals (Palomares and Caro 1999, Janssen et al. 2007, Vance-Chalcraft et al. 2007). This interaction can be the consequence of intense competition for resources resulting in extreme interference competition, or simply opportunistic predation by a larger carnivore on a smaller competitor (Polis et al. 1989). Regardless of the underlying cause, the population-level effects of interspecific killing can be

substantial. It can regulate populations directly but also indirectly affect population dynamics by forcing intraguild prey into marginal habitat to escape predation (Polis and Holt 1992, Mills and Gorman 1997). Interspecific killing has reduced abundance or altered distributions of several sensitive carnivore species throughout the world, including San Joaquin kit fox (*Vulpes macrotis mutica*; White and Garrott 1997, Cypher and Spencer 1998), African wild dog (*Lycan pictus*; Creel and Creel 1996), swift fox (*Vulpes velox*; Thompson and Gese 2007), and Channel Island fox (*Urocyon littoralis*; Roemer et al. 2001).

The fisher (*Pekania [Martes] pennanti*) is a mid-sized carnivore in the family Mustelidae that inhabits coniferous and mixed hardwood-coniferous forests of the western and

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eastern United States, northern Rocky Mountains, and southern Canada (Powell 1981). In California, the fisher historically ranged throughout the mixed coniferous forests of the northwest mountains, through the Cascade Range of north-central California, and south throughout most of the Sierra Nevada, though recent evidence suggests a spatial gap in current range of the fisher in the northern Sierra Nevada may have been present prior to European influence in the region (Tucker et al. 2012). Since the early 1900s, the fisher's range in California has contracted, resulting in 2 strongly spatially isolated populations (Zielinski et al. 2005), 1 in the Coastal Range and Klamath mountains and a much smaller population in the southern Sierra Nevada, estimated at fewer than 300 adult fishers (Spencer et al. 2011). In 2004, fisher populations in the western United States were deemed a candidate for the United States Endangered Species Act of 1973, with the determination that listing was "warranted but precluded" (United States Fish and Wildlife Service 2004). Among the poorly understood threats to fishers is predation, or interspecific killing (United States Fish and Wildlife Service 2004). Intraguild predation and interspecific killing on fishers was known to occur occasionally and presumably limited to otherwise vulnerable individuals (Powell 1993, Powell and Zielinski 1994); however, until this study, the frequency of deaths of healthy adult fishers by other predators and their significance for mortality rates of resident fisher populations were unknown.

Sexes and age classes can experience dissimilar vulnerabilities to different predators (Polis and Holt 1992), and we expected predation-related mortality to differ with sex and age of the fisher. Rates of interspecific killing can also fluctuate temporally as intensity of competition for shared resources changes with seasonal diets (Koehler and Hornocker 1991). Understanding the drivers of interspecific killing, the demographic and seasonal patterns in predation rates, and the species of predators responsible is essential for conservation efforts to mitigate the population-level effects in a vulnerable carnivore population.

We determined the prevalence of interspecific killing of fishers, used molecular analysis to identify predators of fishers, and conducted complete necropsies to identify wounding patterns that could help discriminate among predator species in the absence of genetic analyses. We analyzed the predation frequencies by different predator species in relation to study area, sex, age class, and physical characteristics of the fisher carcasses and predation events to determine differential predation risks and characteristics from different predators. We tested the following hypotheses: 1) female fishers experience greater predation rates than males because females are smaller; 2) female fishers experience predation from smaller species of predators than males because females are smaller; and 3) fishers experience seasonal patterns in predation.

STUDY AREA

We recovered deceased, radiocollared fishers from 3 California research projects between 2007 and 2011. Two were in the southern Sierra Nevada on the Sierra National

Forest, the Sierra Nevada Adaptive Management Project (SNAMP) just south of Yosemite National Park and the Kings River Fisher Project (KRFP) south of SNAMP (Fig. 1). The third project was in northwestern California on the Hoopa Valley Indian Reservation (HVRFP; Fig. 1).

Elevation within SNAMP ranged from 1,000 m to 1,850 m and dominant habitat types included Sierran mixed conifer, montane hardwood conifer, and ponderosa pine (*Pinus ponderosa*; Mayer and Laudenslayer 1988). Elevation within KRFP ranged from 1,100 m to 2,282 m and dominant forest types included montane hardwood conifer, Sierran mixed conifer, and ponderosa pine (Mayer and Laudenslayer 1988). Both the SNAMP and KRFP project areas included small patches of montane chaparral, barren rock, and wet meadows.

The HVRFP project was located within the Klamath physiographic province (Kuchler 1977) of northern California, about 50 km northeast of Eureka, California. Elevation ranged from 98 m to 1,170 m. The dominant habitat types were Douglas-fir (*Pseudotsuga menziesii*) and montane hardwood conifer. Meadows occurred sparsely throughout the HVRFP project area. Mid-sized to large predators potentially able to kill fishers within the 3 project areas included bobcat (*Lynx rufus*), coyote (*Canis latrans*), domestic dog (*Canis lupus familiaris*), mountain lion (*Puma concolor*), black bear (*Ursus americanus*), great-horned owl (*Bubo virginianus*), barred owl (*Strix varia*; at HVRFP only), great gray owl (*S. nebulosa*; at SNAMP and KRFP only), northern goshawk (*Accipiter gentilis*), red-tailed hawk (*Buteo jamaicensis*), and golden eagle (*Aquila chrysaetos*).

METHODS

Fishers were radiocollared and tracked at SNAMP (R. Sweitzer and R. Barrett, University of California, unpublished data), KRFP (Thompson et al. 2011), and HVRFP (Matthews et al. 2011) with primary goals unrelated to this research. Collars were equipped with mortality or activity sensors, allowing us to detect fisher mortalities and recover carcasses as soon after death as possible. We were unable to determine exactly when fishers died because not all fishers were tracked every day, but we recorded the maximum possible time interval between death and carcass recovery based on the last known date of activity of each fisher before observing a mortality signal. In all cases, we photographed the mortality site in detail. We collected data and samples following Wengert et al. (2013) when interspecific killing was suspected as the cause of death (e.g., obvious punctures, partial consumption). We recorded information on the characteristics of the mortality event including patterns of consumption and evidence of caching or burying. Samples included swabs of visible bite wounds, clipped (to avoid fisher DNA in root bulbs) fur from near the bite wounds, swabs of the claws and teeth, and non-fisher hairs left on or near the carcass (Wengert et al. 2013). Though we recorded information on size and shape characteristics of bite marks, we did not use those data in any analyses because environmental conditions, autolysis, and disturbance to the carcasses during killing and consumption often cause

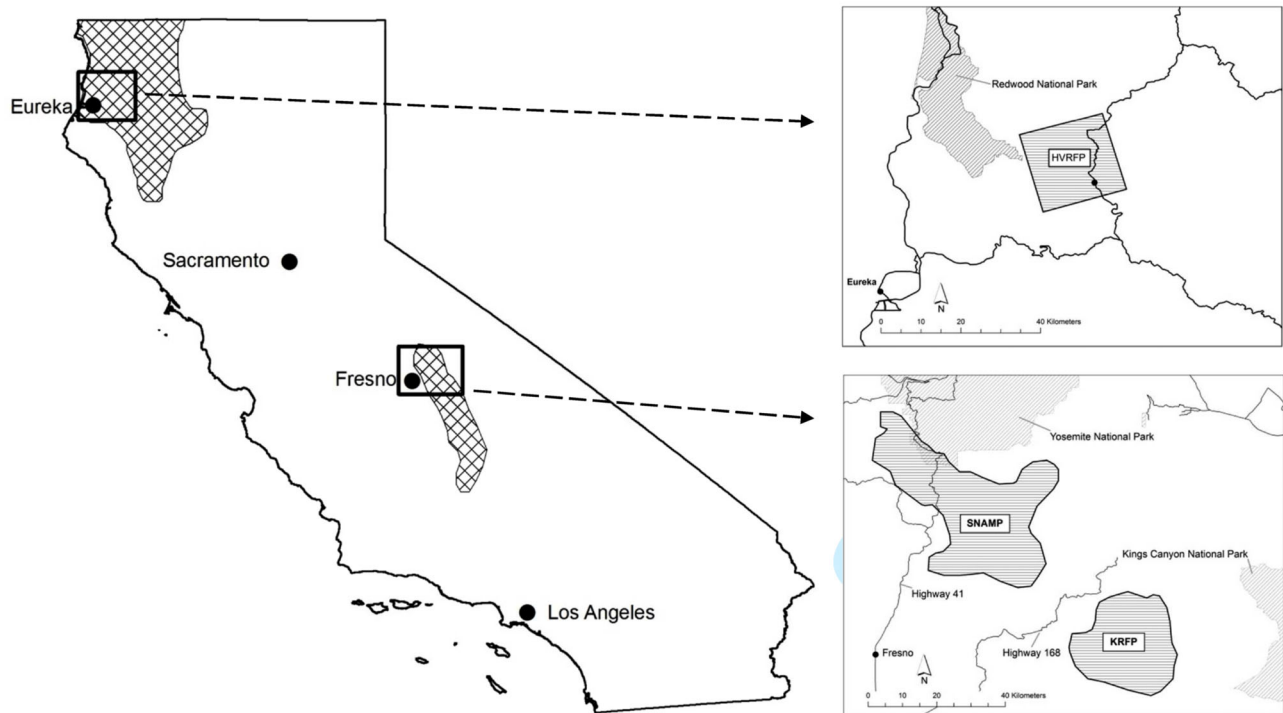


Figure 1. Map of locations of the Hoopa Valley Indian Reservation Fisher Project (HVRFP), Sierra Nevada Adaptive Management Project (SNAMP), and Kings River Fisher Project (KRFP) where we identified predators of fishers (*Pekania [Martes] pennanti*) between 2007 and 2011. Cross-hatched areas of the map represent the fisher's current range in California.

morphological changes in skin and muscle tissue, which may easily result in changing of wound size, spacing, and shape and make accurate identification of predators using these methods unreliable (L. Munson, University of California Davis, School of Veterinary Medicine, personal communication). We double-bagged carcasses in plastic bags and transported them back to the field offices where we froze them in a -20°C freezer until we shipped them to University of California, Davis for further analysis. We obtained weights of each dead fisher from the last capture date prior to death. We calculated time intervals between initial collaring and death due to predation for each fisher. We recorded season of mortality as spring (21 Mar–20 Jun), summer (21 Jun–20 Sep), fall (21 Sep–20 Dec), or winter (21 Dec–20 Mar).

We performed necropsies on all available fisher carcasses either at the University of California Davis, Veterinary Medical Teaching Hospital or California Animal Health and Food Safety Laboratory, Davis, California. When possible, we determined cause of death for each fisher. When we determined interspecific killing to be the cause of death, we described all lesions in detail. We identified the presence or absence of the following lesions on each carcass: depressed skull fractures, full-thickness or subcutaneous-only skull punctures, cervical trauma or fracture, full-thickness or subcutaneous-only punctures in thoracic area or abdominal areas, lacerations in intercostal muscles, and punctures or lesions in extremities. We noted whether the lesions had associated hemorrhage and edema, which indicated ante-mortem wounds likely inflicted by the predator, to

distinguish the wounds from scavenging. In 14 cases, too few remains were present to identify hemorrhage at wound sites, so we conducted only molecular analyses in these cases. We estimated age-classes of the fishers at time of death as either adult (>2 yr of age), subadult (1–2 yr of age), and juvenile (<1 yr of age) based either on tooth wear or cementum annuli counts.

To extract DNA from swabs or matted hair, we used a DNeasy Blood and Tissue Kit (Qiagen, Valencia, CA) and the manufacturer's protocol for blood samples. Specifically, we extracted DNA from $200\ \mu\text{l}$ of a mixture of 1X phosphate-buffered saline solution mixed vigorously with the swab or matted fur sample for 60–90 seconds. We used 2 sets of primers that were family-specific either for Felidae or for Canidae because these were deemed the 2 most likely families of carnivore potentially killing fishers. However, these primers would not amplify Ursid DNA, which was a limitation of this approach. Otherwise, both primer sets amplified the orthologous regions of the mitochondrial genome in hypervariable region I of the D-loop, allowing us to produce sequences to differentiate species within each family (Wengert et al. 2013). We conducted polymerase chain reactions (PCR) in $25\ \mu\text{l}$ reactions, which included $3\ \mu\text{l}$ of DNA template and either 1 U Taq polymerase (Titanium Taq, Clontech, Mountainview, CA), $6\ \mu\text{l}$ of 5X reaction buffer (with MgCl_2), 1.2 mM of total deoxyribonucleotide triphosphates, and primers (i.e., Felid or Canid) at $0.7\text{-}\mu\text{M}$ concentration, or $12.5\ \mu\text{l}$ master mix (GoTaq Green, Promega, Madison, WI) and primers at $0.7\text{-}\mu\text{M}$ concentration. Reactions consisted of an initial denaturation

of 1 minute at 95°C, followed by 36 cycles of 20 seconds denaturation at 95°C, 30 seconds annealing at 55°C (Felidae) or 51°C (Canidae), and 40 seconds extension at 72°C, and final extension of 10 minutes at 72°C.

We electrophoresed PCR products on a 1.0% agarose gel with GelStar (Lonza Group Limited, Basel, Switzerland) as a nucleic acid stain and visualized them using a Dark Reader non-ultra-violet transilluminator (Clare Chemical Research, Inc., Dolores, CO).

We gel-excised the appropriately sized fragment (200–300 bp for felid PCR and 400 bp for canid PCR) and extracted DNA using Qiagen Qiaquick Gel Extraction kit according to the manufacturer's instructions. We sequenced and aligned PCR products using RidomTraceEdit (Ridom GmbH, Würzburg, Germany). We cross-referenced the sequences on GenBank using Basic Local Alignment Search Tool (BLAST) to match them to the most closely aligned sequence to identify species of predator DNA.

We used Student's *t* tests to determine differences in average time to carcass recovery between consumed and unconsumed carcasses, and also differences in average weights between bobcat-killed and mountain lion-killed fishers. We used Chi-square tests of independence or Fisher exact tests as appropriate (Zar 1999) to determine whether certain characteristics of the fisher carcass or predation event were more or less frequently associated with a particular predator species and for determining seasonal patterns in killing. We used analysis of variance ($P=0.05$) to determine differences in average time between collaring and death due to predation among the project areas. All analyses were conducted using program R version 2.14.1 (R Core Team 2012).

RESULTS

From 2007 through 2011, we captured, radiocollared and tracked 188 fishers for which fate was known. Of these, we recovered and analyzed 101 radiocollared fisher carcasses (59 female, 42 male) for cause-specific mortality, of which 62 deaths (61%) were attributed to interspecific killing, either through necropsy or circumstantial forensic information. Forty-three (73%) female deaths and 19 (45%) male deaths were due to interspecific killing. We were able to amplify predator DNA from 50 (81%) of these carcasses (35 females and 15 males), including DNA from bobcat ($n=25$ carcasses), mountain lion ($n=20$), coyote ($n=4$) and 1 carcass with both bobcat and mountain lion DNA. No other carcasses had DNA from more than 1 predator species. We classified all fishers as either adult or subadult at the time of death, except 3 juvenile male fishers and 2 juvenile female fishers at KRFP, and 1 juvenile female and 1 juvenile male fisher at SNAMP. Fisher death was attributed to all 3 predator species at SNAMP and KRFP, but only bobcats and mountain lions at HVRFP (Table 1). Because we found only 4 coyote-killed fishers throughout the 3 study areas, we did not include them in statistical analyses. We also did not include the fisher carcass with both bobcat and mountain lion DNA because we were uncertain which species was the predator. Fishers were killed by bobcats and mountain lions

Table 1. Distribution of killed fishers (*Pekania [Martes] pennanti*) and predator species determined through molecular methods (Wengert et al. 2013) across 3 fisher research projects in California: Sierra Nevada Adaptive Management Project (SNAMP), Kings River Project (KRFP), and Hoopa Valley Reservation Fisher Project (HVRFP) from 2007 to 2011. Numbers in parentheses represent juvenile fishers included in that sample.

Project	Bobcat	Mountain lion	Coyote	Total
SNAMP				
Female	12(1)	1	1	14
Male	0	6(1)	1	7
KRFP				
Female	5(1)	6(1)	1	12
Male	0	4(3)	1	5
HVRFP				
Female	8	0	0	8
Male	0	3	0	3
Total	25	20	4	49

at similar relative frequencies across the 3 study areas ($\chi^2 = 4.76$, $P=0.12$), allowing us to pool data across study areas for further analyses.

All 25 fishers killed by bobcats were female, whereas only 7 of the 20 (35%) fishers killed by mountain lions were female (Table 1). Female fishers were more frequently killed by bobcats than by mountain lions, and male fishers were more frequently killed by mountain lions than by bobcats ($\chi^2_1 = 19.80$, $P < 0.01$; Table 1). Coyotes killed 2 male and 2 female fishers. Weights of fishers at last capture before death were greater for mountain lion-killed fishers than bobcat-killed fishers ($t_{42} = -4.19$, $P < 0.01$) when we pooled the fisher sexes. However, to remove the possible confounding effect of fisher sex, we also analyzed females separately because only females suffered predation from both bobcats and mountain lions. Results for only females indicated no influence of fisher weight on predator species ($t_{7.80} = 1.58$, $P = 0.15$). Predation frequency by mountain lions of juvenile versus adult and subadult fishers did not differ between fisher sexes ($\chi^2_1 = 0.07$, $P = 0.61$). We did not evaluate predation frequency of juveniles between the sexes for bobcats because bobcats did not kill any male fishers.

The highest frequency of interspecific killing occurred during the spring with 29 (47% of all predation mortalities), then fall with 14 (23%), winter with 10 (16%), and summer with 9 (14%). Spring had a significantly higher frequency of interspecific killing than would be expected if interspecific killing were even among the seasons ($\chi^2_3 = 16.58$, $P = 0.001$), but males and females were equally likely to be killed during any season ($\chi^2_3 = 3.72$, $P = 0.29$). Bobcats killed proportionally more fishers during spring relative to mountain lions ($\chi^2_3 = 7.81$, $P = 0.049$).

Predator-killed fishers lived 0.1–6.5 years and an average of 1.13 years (SE = 0.16 yr) after initial collaring. Fishers collared in HVIR lived significantly longer after collaring ($\bar{x} = 2.30$ years, SE = 0.54, $n = 13$) than SNAMP fishers ($\bar{x} = 0.87$ years, SE = 0.14, $n = 27$), and KRFP fishers ($\bar{x} = 0.76$ years, SE = 0.16, $n = 22$; $F_{2,59} = 9.38$, $P \leq 0.001$).

We recovered predator-killed fisher carcasses between 1 and 18 days after death. Time between death and carcass recovery had no influence on whether a carcass was consumed

($t_{51} = -0.41$, $P = 0.69$). Thirty-seven (76%) of the 49 predated fishers for which we identified the predator were partially or mostly consumed, including 22 of 25 (88%) bobcat-killed fishers, 18 of 20 (90%) mountain lion-killed fishers, but none of the 4 coyote-killed fishers (Table 2). Bobcats and mountain lions consumed the fishers they killed with similar frequencies ($\chi^2_1 = 0.07$, $P = 1.000$). Six of the predator-killed fishers (12%) were cached (Table 2). Coyotes cached 3 kills, 1 under snow or snow mixed with duff, and 2 that were almost completely buried beneath soil. Bobcats cached 2 kills under snow or snow mixed with duff, whereas a mountain lion cached 1 fisher under snow.

Thirty-six fisher carcasses exhibited skull trauma, either focal punctures ($n = 10$), depressed (i.e., crushed-bone) skull fractures ($n = 16$), or consumption of most of the skull, leaving only partial jaw bones ($n = 8$), or consumption of the entire skull ($n = 2$). Mountain lions more frequently inflicted depressed skull fractures or left only small pieces of the skull or no skull remaining ($\chi^2_1 = 19.90$, $P < 0.01$) than bobcats (Table 2). Thirteen of 25 (52%) bobcat-killed fishers had fully intact skulls. Of these, cardiac, lung, and tracheal punctures were the apparent causes of death. No mountain lion-killed or coyote-killed fishers had fully intact skulls. Bobcats left the skull fully intact more frequently than mountain lions ($\chi^2_1 = 12.20$, $P < 0.01$). Though fishers killed by all 3 predator species exhibited trauma in the thoracic and abdominal regions, only coyote-killed fishers showed massive hemothorax and intercostal muscle tearing without external punctures in the skin ($n = 3$), most likely related to the violent shaking of the prey often observed during kills by canids.

DISCUSSION

Interspecific killing was the cause of 61% of all fisher deaths we investigated. Other causes of death included disease (both infectious and toxicant-related), vehicular strike, and other human-caused mortality (Gabriel 2013). The proportion of

fisher mortalities caused by predation was greater than reported previously in California (Buck 1982) where 1 of 4 deceased fishers was killed by a predator, in Oregon where 2 of 6 female deceased fishers and 0 of 3 male deceased fishers were killed by predators (Aubry and Raley 2006), in the southern Sierra Nevada of California where 3 of 7 deceased fishers were killed by predators (Truex et al. 1998), and in British Columbia (Weir and Corbould 2008) where 2 of 20 deceased fishers were killed by predators. Powell and Zielinski (1994) suspected that significant rates of predation of healthy adults would occur mainly in translocated fisher populations. In a study of reintroduced fishers translocated from Minnesota to northwest Montana, over half of the fisher deaths were attributed to predation (Roy 1991). Likewise in our study, over half of the fisher deaths were due to interspecific killing; however, ours were native fishers. Our study clearly indicates native populations, including adult fishers, are also susceptible to high rates of mortality from predation.

Radiocollars may influence the risk of mortality (Withey et al. 2001, Thompson et al. 2012). A caveat of our findings, as with any such study, is that we have no way to assess whether the collars themselves could have affected risk of interspecific killing. However, most predation mortalities in this study occurred several months up to several years after collaring, suggesting that predation risk was not related to the capture process itself or within an acclimation period as has been suggested for several other carnivores (Laurenson and Caro 1994, Cypher 1997, Tuytens et al. 2002). Moreover, the lower predation frequencies reported in the studies referenced above also were based on radiocollared fishers. Interestingly, HVRFP fishers lived longer after collaring than fishers in SNAMP or KRFP. This trend could be related to the longer time period over which the HVRFP study has been conducted (since 2005) but might also relate to varying age structures of the 3 populations of collared fishers or differences in predator or prey communities among the study areas.

Table 2. Field and pathologic characteristics of fishers (*Pekania [Martes] pennanti*) killed by bobcat (*Lynx rufus*), mountain lion (*Puma concolor*), or coyote (*Canis latrans*) across 3 fisher research projects in California from 2007 to 2011. Predator species were confirmed using molecular analysis of salivary DNA from bite wounds on the carcasses. Also shown are characteristics of 12 fishers (Pepe51–Pepe62) killed by unknown predator species.

Predator species/fisher	Fisher sex	Consumed	Cached	Depressed skull fracture or skull mostly/fully consumed	Focal punctures in skull	Intact skull	Hemothorax/intercostal muscle tearing
Bobcat ($n = 25$)		22 (88%)	2 (8%)	6 (24%)	5 (20%)	13 (52%)	0
Mountain lion ($n = 20$)		18 (90%)	1 (5%)	19 (95%)	1 (5%)	0	2 (10%)
Coyote ($n = 4$)		0	3 (75%)	1 (25%)	3 (75%)	0	3 (75%)
Pepe 51	F	YES	NO	YES	NO	NO	NO
Pepe 52	F	NO	NO	NO	NO	YES	NO
Pepe 53	F	NO	YES	NO	NO	YES	YES
Pepe 54	F	YES	NO	NO	NO	YES	NO
Pepe 55	F	NO	YES	NO	NO	YES	NO
Pepe 56	M	NO	NO	NO	NO	NO	NO
Pepe 57	M	NO	YES	NO	YES	NO	YES
Pepe 58	M	NO	NO	NO	YES	NO	YES
Pepe 59	M	NO	NO	NO	YES	NO	NO
Pepe 60	F	YES	NO	NO	NO	YES	NO
Pepe 61	F	YES	NO	NO	NO	YES	NO
Pepe 62	F	YES	YES	NO	NO	YES	NO

The species we identified as predators of fishers (mountain lions, bobcats, and coyotes) differ from those suspected of killing fishers in prior California accounts (Grinnell et al. 1937, Buck 1982, Buck et al. 1983) and in other areas throughout their range (Roy 1991, Krohn et al. 1994, Vashon et al. 2002, Weir and Corbould 2008). Bobcats were the most frequent fisher predator in our study but not previously reported to prey on fishers. Conversely, we found coyotes to be an infrequent predator of fisher, whereas coyote was the most frequently cited predator of fisher in the literature (Buck 1982, Roy 1991, Krohn et al. 1994, Aubry and Raley 2006). Similarities between our study and previous accounts of predation on fishers are limited to those studies identifying mountain lions as fisher predators (Grinnell et al. 1937, Aubry and Raley 2006). Other predators suspected of killing fishers in other regions with different predator communities include wolverine (*Gulo gulo*) and Canada lynx (*Lynx canadensis*; Roy 1991, Weir and Corbould 2008), golden eagle (Roy 1991), great-horned owl (Buck et al. 1983), and other fishers (Buck 1982, Weir and Corbould 2008).

Ours is the first study to use DNA to verify predators and differentiate predator species of fishers. Differences in findings with studies from other locations with different predator communities, however, are not surprising, such as those finding wolverine or lynx as predators of fisher (Roy 1991, Weir and Corbould 2008). Furthermore, fishers in California are thought to be smaller than in other areas of their range (Powell 1993), ostensibly making them more vulnerable to predation by smaller predators, such as bobcats versus just coyotes and mountain lions implicated in other studies. Other factors could explain differences in predator species observed to prey on fisher in different times and places, including dissimilar relative densities of different predator species or predator-fisher ratios. Finally, different habitat types and features at the 3 projects might subject fishers to greater risk of predation by a particular predator species with, for example, a greater penchant for hunting or traveling within certain habitat features, as shown in other canid and felid predator communities (Brown and Litvaitis 1995, Murray et al. 1995, Karanth and Sunquist 2000).

Predators of 12 carcasses we investigated could not be identified by the molecular approach, either because of insufficient DNA, advanced autolysis of the carcass, or because the predator species was not canid or felid. None of the predator-killed fishers in our study displayed forensic characteristics consistent with killing by another fisher (Weir and Corbould 2008) or raptor predation, such as degloving (stripping skin inside out along bone) or symmetrical talon marks (Coonan et al. 2005). Unfortunately, our methods were only able to detect felid and canid DNA, and were unable to detect black bear DNA, so black bear killing of fishers with subsequent scavenging by canids or felids would go undetected. Nevertheless, even if all unassigned cases were attributed to bear, this would imply a maximum of 19% of cases to bear predation, which was clearly less significant than that owing to the 2 felids.

We found that female fishers were more likely to be killed by bobcats and male fishers were more likely to be killed by mountain lions. Similarly, in a reintroduction of fishers in Montana, Roy (1991) found that mountain lions only killed male fishers ($n = 3$), although coyotes killed both male and female fishers. Also in that study, 2 female fishers were killed by golden eagle and Canada lynx (Roy 1991). Their findings were similar to Weir and Corbould (2008) and Buck (1982) who determined Canada lynx and raptors, respectively, to be responsible for female fisher deaths. This dichotomy in sex-specific predation by different predator species probably stems from the pronounced sexual size dimorphism between male and female fishers. In our study, weights of male fishers killed by predators ranged from 2.0 kg to 4.5 kg falling at the high end of the typical size range for bobcat prey, whereas female fishers ranged from 1.55 kg to 2.4 kg, well within typical prey size range for bobcats (Anderson and Lovallo 2003). Although we found differences in the weights of fishers killed by mountain lions and fishers killed by bobcats when fisher sexes and ages were combined, we could not attribute this solely to weight because we did not assess other characteristics that potentially differ between female and male fishers (i.e., greater movement by males, differential habitat use by the sexes) that could affect their respective vulnerabilities to these predator species.

Mountain lions typically take larger prey than do bobcats (Leopold and Krausman 1986, Koehler and Hornocker 1991). Perhaps the significantly lower energetic value of a female fisher at least partly contributes to this trend, although the diet of mountain lions in the southern Sierra Nevada can include a large percentage of small mammal prey (Neal et al. 1987). Alternatively, male fishers, with their significantly larger home ranges and potentially different patterns in habitat use may also be more likely to cross paths with mountain lions than females, leading to greater risk of interaction. Though our results indicated greater likelihood of female fisher predation by bobcats relative to other predator species, we noted an emerging trend in the final 2 years of our study at KRFP of more frequent predation on female fishers by mountain lions. Of the 6 female fishers killed by mountain lions, 5 occurred in late 2010 through 2011. Such local and temporal trends may be explained by any number of factors, including a particular individual tendency. Habitual behavior has been documented in individual mountain lions repeatedly killing porcupines (*Erethizon dorsatum*; Sweitzer et al. 1997) or bighorn sheep (*Ovis canadensis*; Ernest et al. 2002), and specialist mountain lions in Patagonia (Elbroch and Wittmer 2013).

Regardless, female fisher predation was mostly attributed to bobcats. Fisher kits are completely dependent on their mothers for survival during March through July (Powell 1993), when over 70% (19 of 25) of female predation deaths by bobcats occurred. Therefore, bobcat predation in particular is likely to affect the population dynamics of fishers. Interestingly, spring might be a time when female fishers are more active and concentrate greater movements closer to their den sites (Powell 1993), so it is not likely increased space use during the denning season that

predisposes them to bobcat predation. Rather, we suggest that additional research is needed to explore from the perspective of bobcat ecology the prey base, habitat, and other ecological characteristics that could increase risk of bobcat predation on fishers. Understanding what factors drive bobcat predation on fishers is an important question with respect to our ability to manage this potentially influential mortality factor.

Coyotes did not consume any fisher carcasses but did cache 3 of 4 fisher carcasses. It is possible that coyotes cached the carcasses with the intent to consume the prey at a later time had field biologists not removed the fisher carcasses from the cache sites. Bobcats and mountain lions seldom cached the fisher carcasses (2 of 25 and 1 of 20, respectively). That both bobcats and mountain lions consumed fishers suggests they were killed as prey rather than competitors. However, in the 1 instance that the mountain lion killed but did not eat the fisher, the carcass was found very near a recently killed deer carcass suggesting that the fisher was killed for competitive reasons while investigating or consuming the lion's cache. Finally, in several cases, we found too few remains to detect hemorrhage, which would verify predation rather than scavenging. We believe a majority of these cases were direct predation because 1) we found DNA from more than 1 predator species (suggesting 1 of them scavenged) on only 1 carcass, 2) in 2 of these cases, the remains were cached, a behavior typically done for prey that is killed, and 3) in about half these cases, the carcass was reached within a day of death leaving little time for a would-be scavenger to find and consume the carcass. Furthermore, if bobcats were scavenging female fisher carcasses, they also would likely scavenge and leave DNA on male fisher carcasses for which we found no evidence.

MANAGEMENT IMPLICATIONS

Managing and conserving fishers in western populations requires an understanding of the threats to their persistence. Until now, interspecific killing would not have been high on the list of pressing threats. Our results show higher frequency in interspecific killing as a mortality source for fishers than was previously documented. In their evaluation of the status of the southern Sierra Nevada fisher population, Spencer et al. (2011) proposed that even minor decreases of only 10–20% in survivorship of this fisher population due to increases in any type of mortality could prevent expansion northward into currently unoccupied portions of their former range. Because we found that interspecific killing is the most common cause of mortality of fisher in these study areas, fluctuations in fisher mortality due to interspecific killing could constitute increases in mortality sufficient for population limitation. Our findings also highlight the heretofore unknown and potentially critical impact of bobcat predation on female fishers, especially during the denning season.

Management of fisher habitats and conservation plans should take into consideration predation risks to fishers by bobcats as well as mountain lions and other predators. The high percentage of fisher mortality caused by predation,

particularly from bobcats and mountain lions, and the apparent potential of such mortality to influence fisher population dynamics demonstrates the importance of further study of fisher, bobcat, and mountain lion habitat use and selection, especially in relation to habitat manipulation by humans. With the knowledge that California fisher populations face high rates of mortality and reductions in survival from bobcat predation, forest managers may consider habitat management that favors fishers while minimizing habitat features that favor bobcats or mountain lions where they coexist with fishers. Moreover, additional research is needed to explore habitat characteristics that may encourage or discourage bobcat predation on fishers, potentially providing managers with specific tools that can be used to manipulate habitat in favor of fisher survival, especially during the spring.

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