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Combined field and clinical methods clarify mortality causes and survival patterns of Pacific martens

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Abstract

Quantifying the demography of wildlife populations is imperative to evaluating population trends. Understanding patterns of influential demographic parameters often requires investigation of mechanisms influencing demography, which can be difficult to determine for cryptic species. We radio-tracked Pacific martens (*Martes caurina*), a small-bodied and elusive mesocarnivore, to estimate survival, determine causes of mortality, and assess co-occurring pathological conditions. We tracked 18 female and 33 male martens for an average (±SD, range) of 16.35 months (±8.7, 1–41) from 2009–2013 and 2015–2017 in northern California. Annual survival rates were 0.81 (95% CI = 0.66–0.95) and 0.68 (95% CI = 0.57–0.79) for female and male martens, respectively. We documented 16 marten mortalities, 13 of which were suspected predation events. Seven mortalities were empirically linked to predation via clinical forensic evidence, with bobcats (*Lynx rufus*; $n = 5$) representing the majority of predator species identified. The proximate cause of mortality for 1 marten was attributed to toxicosis from anticoagulant rodenticide exposure, which has not been previously reported in free-ranging martens. Our findings suggest the timing of marten mortality aligned with reproductive periods that incurred increased energetic requirements, which may result in increased predation risk. We propose continued pairing of field and clinical assessments to

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better substantiate mortality sources of wildlife, elucidate underlying pathology, and identify novel stressors.

KEYWORDS

bobcat, intraguild predation, known-fates, *Martes caurina*, mustelid, population ecology, survival, wildlife forensics

Quantifying demographic parameters is required to evaluate dynamics of wildlife populations (Buckland et al. 2000, Eberhardt 1985) and guide management practices intended to better conserve species or populations of interest. At-risk species may be particularly sensitive to demographic or environmental stochasticity (e.g., climate change, habitat loss; McLean et al. 2016) and understanding the relative importance of demographic parameters, such as survival, can clarify current population trends and predictions of future population conditions (Baker and Thompson 2007, Glenn et al. 2010). Identifying factors that cause variation in survival can further link external interactions to fitness (Skalski et al. 2005). The influence of survival on population demography can be particularly consequential for species with slow life histories (Promislow and Harvey 1990), characterized by traits such as delayed sexual maturity, low reproductive outputs, and low population growth rates (Dobson and Oli 2007). But species that are rare, cryptic, or occur at naturally low densities are often difficult to observe, leading to increased difficulty in elucidating population trends (Thompson 2013).

North American martens (American marten [*Martes americana*], Pacific marten [*M. caurina*]) are small-bodied (500–1,400 g; Nagorsen 1994), elusive mesocarnivores that exhibit some slow life-history strategies. For example, female martens do not reach sexual maturity until the age of 2, typically produce small litters of 2–3 kits (Delheimer et al. 2021), and may not reproduce every year after achieving sexual maturity. Unlike many other species exhibiting slow life histories, martens have relatively short lifespans in free-ranging conditions (typically ≤ 5 yr), and, consequently, the survival of sub-adult and adult martens influences population growth and persistence (Buskirk et al. 2012). There are also important sex-specific differences in marten behavior and physiology that may influence survival but have not been explicitly tested. For example, male martens are larger-bodied, have larger home ranges, and often exhibit higher energetic expenditures relative to female martens (Moriarty et al. 2017, Martin et al. 2020). Martens are often polygynandrous, where male martens typically attempt to mate with as many females as possible during a relatively brief mating period (i.e., Jul–Aug; Ruggiero and Henry 1993), whereas females incur the costs of pregnancy and kit-rearing (i.e., Mar–Jul; Delheimer et al. 2021). Though research suggests these aspects of animal behavior, physiology, and ecology may affect survival patterns (Promislow 1992, Mills 2007), inferences about the mechanisms influencing marten survival are often constrained by small sample sizes, variable estimates (Table 1), and uncertainty regarding sources of mortality.

Like many carnivores in North America, marten populations have experienced local (Zielinski et al. 2005) and continental (Laliberte and Ripple 2004) declines in distribution and abundance due to forest loss and fragmentation and over-harvest for the fur trade during the nineteenth and twentieth centuries (Laliberte and Ripple 2004). Continued habitat modification (e.g., forest thinning to reduce fire risk; Zielinski 2014, Moriarty et al. 2016) and emerging stressors, including shifts in climatic conditions (Mote et al. 2005, Millar et al. 2007) and wildfire regimes (Jones et al. 2016), can affect the behavior or movement of martens (Moriarty et al. 2015). Because of their long, thin body shape, martens exhibit a high surface area-to-body-mass ratio that results in relatively high metabolic rates (Brown and Lasiewski 1972, Buskirk and Harlow 1989) and precludes the ability to accumulate substantial fat depots. Consequently, martens must frequently forage to avoid starvation (Gilbert et al. 2009) and their behavior and energetic expenditures are sensitive to changes in community and forest structure (Moriarty et al. 2016, Martin et al. 2020).

Because of their small size and subordinate status, martens are more susceptible to intraguild predation than other carnivores (Palomares and Caro 1999). Predation is reported as a substantial source of natural mortality in

TABLE 1 North American marten (American marten and Pacific marten) annual adult survival rates from populations not subject to trapping harvest. For 2 studies, we included 2 survival estimates to represent independent study areas (Thompson 1994, Payer and Harrison 1999)

Sex	Location	*n*	Survival (95% CIs)	Source
Female				
	Ontario	8	0.89 (0.68–1.00)	Thompson (1994)
	California	18	0.81 (0.66–0.95)	This study
	Maine	29	0.81 (0.65–1.00)	Payer and Harrison (1999)
	Wisconsin	12	0.77 (–)	McCann et al. (2010)
	Wisconsin	8	0.74 (–)	Woodford et al. (2013)
	Oregon	18	0.67 (0.18)	Wilk and Raphael (2018)
	Maine	17	0.62 (0.32–1.00)	Payer and Harrison (1999)
	Ontario	8	0.61 (0.06–1.00)	Thompson (1994)
	Maine	33	0.53 (0.34–0.83)	Hodgman et al. (1997)
Male				
	Maine	32	0.95 (0.85–1.00)	Payer and Harrison (1999)
	Ontario	14	0.92 (0.76–1.00)	Thompson (1994)
	Maine	26	0.87 (0.75–1.00)	Hodgman et al. (1997)
	Wisconsin	22	0.85 (–)	McCann et al. (2010)
	Maine	26	0.84 (0.72–0.98)	Payer and Harrison (1999)
	Wisconsin	10	0.79 (–)	Woodford et al. (2013)
	California	33	0.68 (0.57–0.79)	This study
	Oregon	35	0.67 (–)	Wilk and Raphael (2018)
	Ontario	7	0.43 (0.00–1.00)	Thompson (1994)
Combined sex				
	Ontario	22	0.91 (0.78–1.00)	Thompson (1994)
	Wisconsin	34	0.81 (–)	McCann et al. (2010)
	California	51	0.74 (0.65–0.83)	This study
	Oregon	53	0.68 (–)	Wilk and Raphael (2018)
	Oregon	35	0.64 (–)	Bull and Heater (2001)
	Ontario	15	0.54 (0.08–0.99)	Thompson (1994)

untrapped marten populations (>70% of marten deaths; McCann et al. 2010, Wilk and Raphael 2018) and martens are commonly killed by terrestrial carnivores, including bobcats (*Lynx rufus*), coyotes (*Canis latrans*), and fishers (*Pekania pennanti*; Figure 1; Table S1, available in Supporting Information). Though avian predation is also relatively common, avian predators of martens are rarely identified to species (McCann et al. 2010). Predation is a clear source of mortality for martens, but predation as an event, or the identity of a predator species, is often assumed based on field assessments (e.g., apparent bite wounds, tracks, scat; Gabriel et al. 2015) rather than through more robust methods including confirmation by molecular techniques (Wengert et al. 2013). Distinguishing between

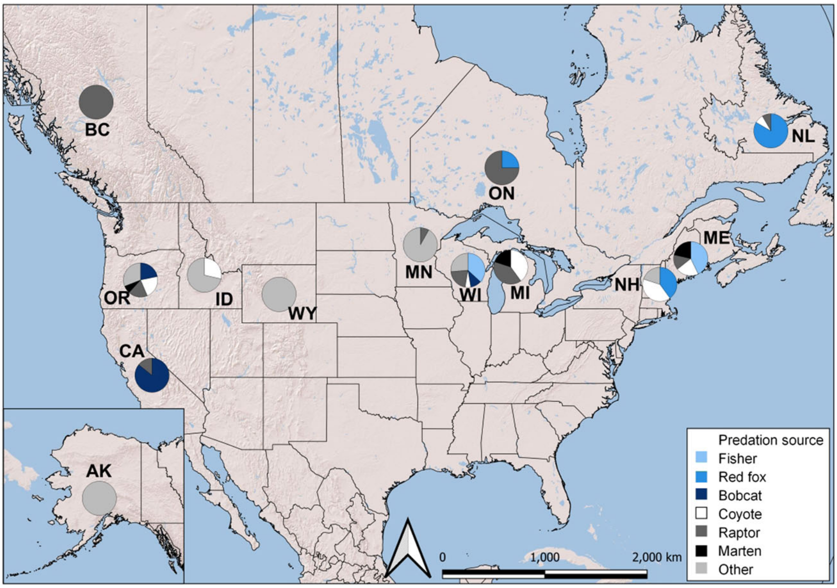

FIGURE 1 Predators of North American martens (American marten and Pacific marten) as reported in literature published from 1994 to 2021. We used raptor to represent avian predators that were rarely identified to species. We used other for species that were infrequent predators (i.e., <1 reported instance of predation) or unknown mammals

scavenging and predation can be difficult in field-based assessments of mortality and typically requires conducting a necropsy (Wengert et al. 2012). Thus, predation is infrequently validated and often misclassified in field studies of wildlife mortality (Wengert et al. 2012, 2013).

Though predation is often reported as a leading cause of mortality in free-ranging martens (Figure 1; Table S1), the prevalence of causes of marten mortality other than predation ranges from poorly understood to completely unknown. However, cryptic causes of mortality or morbidity could be determined with clinical methods. For example, during field assessments of mortality in a fisher population in California, USA, mortalities were attributed to varied factors including drowning, collar strangulation, and negative reactions to anesthesia (Gabriel et al. 2015). Further investigation in a clinical setting indicated all of these events were caused by, or related to, disease, reinforcing the importance of applying clinical methods to identify mortality causes (Gabriel et al. 2015). Clinical assessments of animal carcasses also provide the opportunity to identify the effects of contemporary human activities, such as the use of anticoagulant rodenticides, on animal health and survival (Gabriel et al. 2015). Anticoagulant rodenticides globally imperil the health of wildlife communities (Van den Brink et al. 2018) and their use has been banned or significantly regulated by many states in the western United States (California Legislative Assembly 2020). Because of the continued use of anticoagulant rodenticides in illegal cannabis production in the United States, wildlife species are often exposed to rodenticides and exposure is an emerging source of mortality for species of conservation concern, including federally threatened fishers (Gabriel et al. 2012, 2015) and northern spotted owls (*Strix occidentalis caurina*; Wiens et al. 2019). Anticoagulant rodenticides have the potential to similarly harm martens, but their effect or rate of exposure has not been documented for martens.

Our objectives were to evaluate survival patterns and causes of mortality and morbidity in a free-ranging population of Pacific martens in northern California. Specifically, we hypothesized that survival of martens could be explained by intrinsic (i.e., sex) and extrinsic (i.e., time) factors. By identifying factors that influence survival rates and robustly assessing proximate causes of marten mortality through field and clinical techniques, we address continued information gaps and provide guidance for future research.

STUDY AREA

Our study occurred at the interface of the Cascade and Sierra Nevada mountain ranges in northeastern California from 2009–2013 and 2015–2017 at 2 sites on lands administered by the United States Department of Agriculture (USDA) Forest Service, Lassen National Forest (Figure 2), which supports recreational activities, timber harvest, and cattle grazing. Our 397-km^2 study area was characterized by steep and varied topography, with elevation ranging from 1,550–2,200 m, and climate was characterized by short, dry summers (Jun–Sep) and cool, wet winters (Dec–Mar). Annual mean precipitation ranged from 50 cm to 200 cm, with precipitation typically falling as snow from October–March, and mean snow depth in April was 114 cm (California Data Exchange Center 2018). During snow-free periods, average minimum, mean, and maximum temperatures were 12°C, 17°C, and 22°C, respectively. During snow-covered periods, average minimum, mean, and maximum temperatures were 3°C, 6°C, and 11°C, respectively (California Data Exchange Center 2018, Oct 2009–Feb 2013, Oct 2015–Nov 2017). Forested stands were mesic and typified by red (*Abies magnifica*) and white firs (*A. concolor*), with a variety of interspersed pine species (*Pinus* spp.). Forest openings included sub-alpine meadows, regenerating clear-cuts, and shrub fields dominated by chinquapin (*Chrysolepis chrysophylla*), deer brush (*Ceanothus intergerrimus*), mountain whitethorn (*C. cordulatus*), tobacco brush (*C. velutinus*), and white (*Arctostaphylos manzanita*) and green leaf manzanita (*A. patula*). The study area supported a rich faunal community, including many mammalian carnivores, such as black bear (*Ursus*

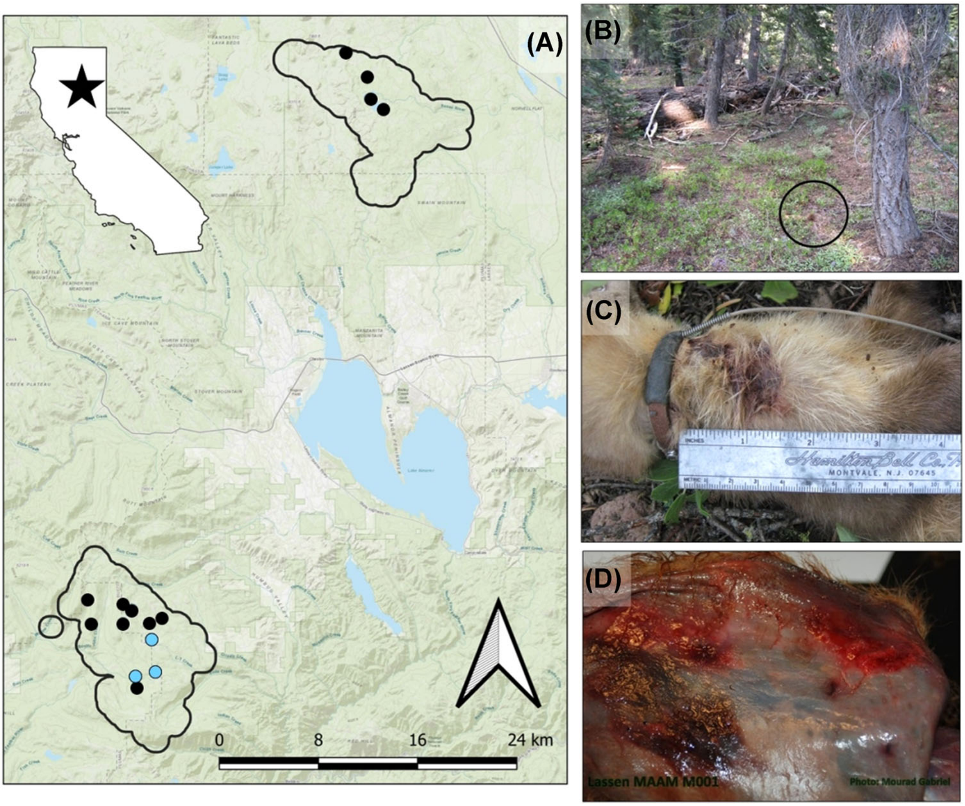

FIGURE 2 We documented 16 mortalities (*n* = 4 females [blue circles], *n* = 12 males [black circles]) from radio-collared Pacific martens monitored on study areas (black poloygons) in Lassen National Forest, California, USA (A). Using a forensic protocol, we evaluated the suspected mortality scene (e.g., black circle in panel B), collected samples (panel C), and completed a full necropsy and clinical assessment of the mortality (panel D)

americanus), bobcat, cougar (*Puma concolor*), coyote, long-tailed weasel (*Mustela frenata*), Pacific marten, striped skunk (*Mephitis mephitis*), and western spotted skunk (*Spilogale gracilis*). We also observed a number of cervids, leporids, rodents, including mule deer (*Odocoileus hemionus*), elk (*Cervus canadensis*), snowshoe hare (*Lepus americanus*), Douglas' squirrel (*Tamiasciurus douglasii*), golden-mantled ground squirrel (*Callospermophilus lateralis*), California ground squirrel (*Otospermophilus beechyi*), and chipmunk (*Neotamias* spp.). Non-mammalian fauna were also common, and ranged from songbirds (e.g., western tanager [*Piranga ludoviciana*], Steller's jay [*Cyanocitta stelleri*]), raptors (e.g., northern goshawk [*Accipiter gentilis*]), and galliforms (e.g., mountain quail [*Oreortyx pictus*]) to invertebrates (e.g., zerene fritillary [*Speyeria zerene*], Juba skipper [*Hesperia juba*]) to reptiles and amphibians (e.g., common sagebrush lizard [*Scleropus graciosus*], Sierran tree frog [*Pseudacris sierra*]).

METHODS

We captured martens using modified Tomahawk live traps (model 106, Tomahawk, Hazelhurst, WI, USA). We immobilized martens using an intramuscular injection of a ketamine-midazolam mixture (Mortenson and Moriarty 2015) and recorded sex, mass, and other morphometric measurements. We estimated the age class of martens (juvenile: <1 yr, sub-adult: 1–2 yr, adult: ≥2 yr) based on reproductive status, tooth wear, and sagittal crest development (Poole et al. 1994). We fit martens identified as sub-adult or adult with very-high frequency (VHF; MI-2, Holohil Systems, Carp, Ontario, Canada or M1800, Advanced Telemetry Systems, Isanti, MI, USA) or global positioning system (GPS; Quantum 4000 MicroMini, Telemetry Solutions, Concord, CA, USA or G10 UltraLite GPS Logger, Advanced Telemetry Systems) collars. We programmed collars to emit a fast pulse if the collar had not moved for ≥12 hours. We tracked collared martens year-round and located each marten at least weekly to determine their status (e.g., alive, dead, missing).

We incorporated live-capture and VHF- or GPS-collar tracking data to estimate marten survival by creating individual encounter histories at a monthly sampling frequency. Because of small sample sizes, and to maintain consistency with previous studies of marten survival (Wilk and Raphael 2018), we pooled sub-adult and adult individuals (i.e., all animals ≥1 yr old) to estimate marten survival. To test hypotheses about the effects of time and sex on marten survival, we constructed known-fate models in Program MARK (White and Burnham 1999). Given potential sex-specific variation in survival rates of martens (Table 1), we included a group-level effect for sex within our candidate model set and further included the effects of month and year on survival. We ranked candidate models using Akaike's Information Criterion corrected for small sample sizes (AIC_c; Burnham and Anderson 2002) and determined statistical significance based on 95% confidence intervals. We considered models with $\Delta AIC_c < 2$ to have substantial statistical support and models with $\Delta AIC_c < 4$ to have moderate statistical support (Burnham and Anderson 2002). We implemented a staggered-entry Kaplan-Meier approach (Pollock et al. 1989) to estimate monthly and cumulative annual marten survival. Martens entered the dataset upon capture and were removed upon confirmation of mortality; we censored animals that we could no longer track but could not confirm as dead (e.g., collar failure, dropped collar). For monthly and annual survival estimates, we determined standard error and lower and upper 95% confidence intervals.

When a mortality signal was noted, we tracked the signal to the collar's location, where we subsequently retrieved the marten carcass and conducted field-based assessments if we suspected predation (Wengert et al. 2012). We examined each carcass for injuries consistent with predation, such as bite punctures, missing or damaged extremities, or external hemorrhaging. We clipped and collected fur that was matted with suspected predator saliva or blood, measured bite wound punctures, swabbed punctures to capture predator saliva, and identified any other physical evidence in the vicinity of the carcass (e.g., whitewash, scat, tracks) that would indicate the presence of a predator (Wengert et al. 2012). We recorded geographic coordinates of the carcass and photographed all visible bite wounds, the location of the carcass, and the location of other physical evidence of predation relative to the carcass. We stored carcasses in plastic bags and froze them at −40°C if a necropsy could not be completed immediately.

We determined proximate causes of mortality via gross necropsy, histopathology, molecular analysis of bite wound swabs and fur samples, and toxicology testing (Wengert et al. 2012, 2013). When possible, we also identified ultimate causes of mortality; gross necropsies involved both an external examination and internal examination of the carcass and its viscera for any deviations from homeostasis, which includes the determination of ante-or post-mortem hemorrhaging, to distinguish between predation or scavenging as the cause of injuries (Wengert et al. 2012). We examined tissue samples for any gross or histological changes that indicated infectious or non-infectious disease contributed to morbidity or mortality (Wengert et al. 2012). We extracted DNA from forensic samples using a modified version of the DNeasy Blood and Tissue Kit (Qiagen, Valencia, CA). We analyzed samples for presence of predator DNA and species identification through conventional polymerase chain reaction (PCR) using canid-specific and felid-specific primers and electrophoresed the PCR products on a 1.0% agarose gel (Wengert et al. 2013). We excised 1–2 of the strongest gel bands from each carcass (~200–300 base pairs for felids and 300–400 base pairs for canids) and gel-extracted them using the Qiagen Gel Extraction kit according to the manufacturer's instructions. We aligned and cross-referenced sequences of the PCR products on GenBank using the basic local alignment search tool to determine closest match to published species sequences. Additional details can be found in Wengert et al. (2013).

We also tested liver samples from marten carcasses to assess exposure to anticoagulant rodenticides. It can be difficult and dangerous to test for exposure in living animals because performing a liver biopsy may release sequestered toxicants into the blood stream and result in death due to toxicosis and coagulopathy (Van den Brink et al. 2018). We screened liver samples for presence of anticoagulant rodenticides using liquid chromography-tandem mass spectrometry and quantified positive samples using high-performance liquid chromatography (Gabriel et al. 2012). We tested for first-generation anticoagulant rodenticides including warfarin, diphacinone, chlorophacinone, and coumachlor and second-generation anticoagulant rodenticides including brodifacoum, bromodiolone, and difethialone (Gabriel et al. 2012).

RESULTS

We tracked 18 female and 33 male collared martens from October 2009–February 2013 and October 2015–November 2017. We tracked martens for an average (± SD, range) of 16.35 months (±8.7, 1–41). Survival estimates were relatively high with female and male annual averages (95% CI) of 0.81 (0.66–0.95) and 0.68 (0.57–0.79), respectively (Table 1). Our highest-ranking survival model included the effect of month on survival, with no other competitive models (Table 2). Though 95% confidence intervals of survival estimates overlapped between sexes and among months, we did observe marginal differences in survival rates between months and sexes. Monthly survival of female martens was lower in April (0.89 [0.71–1.00]; Figure 3) than other months. Male survival was lower in July (0.90 [0.78–0.97]) and August (0.79 [0.57–0.83]; Figure 3). Sex-specific annual survival was lower for male martens than female martens (Figure 4).

We documented 16 mortalities (*n* = 4 females, *n* = 12 males) from 2010–2012 and 2016–2017 (Table 3). Female mortalities occurred in February (*n* = 1), April (*n* = 2), and October (*n* = 1), and male mortalities occurred in July (*n* = 4), August (*n* = 7), and September (*n* = 1). Of 16 mortalities, 14 carcasses were submitted for clinical investigations and 2 were not submitted because they were completely consumed and no remains were available for a necropsy or forensics (Table 3). We were able to conduct necropsies on 5 of the 14 carcasses submitted; 9 carcasses had insufficient tissue for necropsy, precluding further testing for disease or anticoagulant rodenticide exposure. We conducted forensics on all submitted carcasses (12 of 14) that were suspected as predation or could not clearly be attributed to another source.

TABLE 2 Model selection results for a known-fate analysis to test hypotheses about the effects of sex, month, and year on survival (Φ) of Pacific martens monitored in Lassen National Forest, California, USA, from October 2009–February 2013 and October 2015–November 2017. We included Akaike's Information Criterion corrected for small sample size (AIC_c), difference in AIC_c score between the top-ranking and subsequent models (ΔAIC_c), model weight (AIC_c ω), model likelihood, and number of parameters included in the model

Model	AIC_c	ΔAIC_c	AIC_c ω	Likelihood	Parameters
Φ(month)	160.56	0.00	0.89	1.00	12
Φ(sex × month)	165.58	5.02	0.07	0.08	24
Φ(null)	168.06	7.50	0.02	0.02	1
Φ(sex)	169.24	8.68	0.01	0.01	2
Φ(year)	170.14	9.57	0.01	0.01	8
Φ(sex × year)	175.95	15.39	0.00	0.00	16

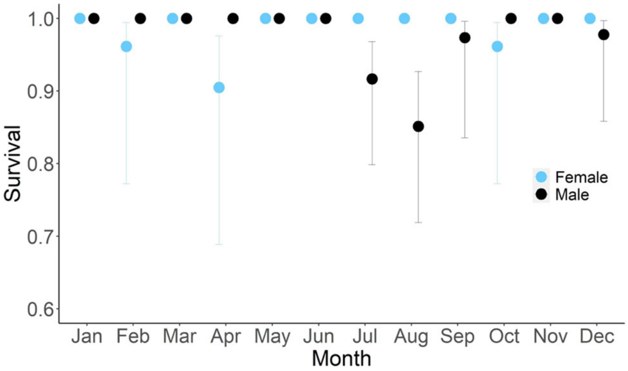

FIGURE 3 Monthly survival estimates (±95% CIs) from 51 adult Pacific martens in Lassen National Forest, California, USA, October 2009–February 2013 and October 2015–November 2017, by sex and month

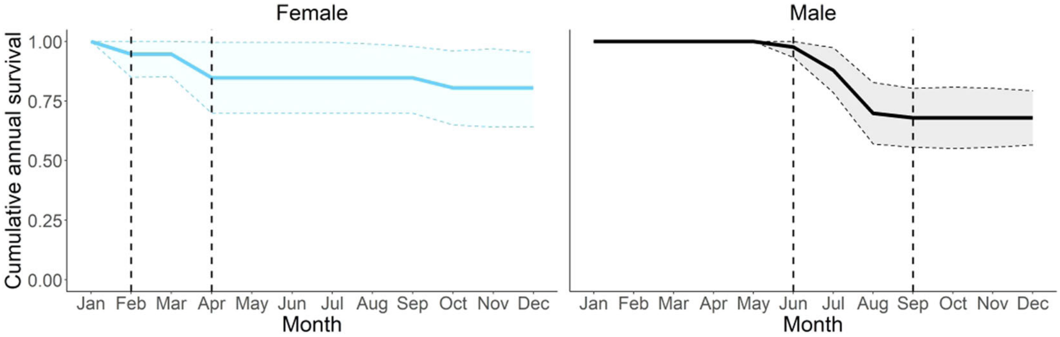

FIGURE 4 Sex-specific cumulative annual survival (±95% CIs) curves of adult Pacific martens in Lassen National Forest, California, USA, October 2009–February 2013 and October 2015–November 2017. Vertical dashed lines highlight sex-specific peaks in mortality, which correspond to sex-specific reproductive periods

TABLE 3 Mortality sources of female (F) and male (M) Pacific martens monitored from 2010–2013 and 2015–2017 in Lassen National Forest, California, USA. We assigned preliminary field assessments of cause-of-death (COD) from physical evidence at carcass locations (e.g., partial or complete consumption of the carcass, presence of bite wounds, scat or whitewash from putative predator species). We attempted to confirm proximate COD via forensics and necropsies (e.g., polymerase chain reaction [PCR] analysis for predator DNA, gross or histological examinations, toxicology testing) when sufficient tissue was available

Marten	COD – field assessment	Field evidence	COD – clinical determination	Clinical evidence	Forensics (yes [Y] or no [N])	Necropsy (yes [Y] or no [N])
F03	Entrapment	Carcass found in underground tunnel	Entrapment	Dehydration, renal failure	Y	Y
F06	Predation	Consumption of carcass, puncture wounds	Predation – bobcat	PCR analysis – bobcat primer hits	Y	N
F08	Predation	Puncture wounds	Predation – bobcat	PCR analysis – bobcat primer hits	Y	N
F18	Predation	Consumption of carcass	Predation – felid	PCR analysis – felid spp. primer hits	Y	Y
M02	Predation	Consumption of carcass, puncture wounds	Predation – bobcat	PCR analysis – bobcat primer hits	Y	N
M04	Predation	Consumption of carcass	Predation (unconfirmed)	PCR analysis – no primer hits	Y	N
M06	Unknown	None – carcass was intact	Toxicosis	Coagulopathy due to brodifacoum (0.74 ppm) and difethialone (0.06 ppm)	N	Y
M08	Predation	Consumption of carcass	Predation (unconfirmed)	PCR analysis – no primer hits	Y	Y
M09	Predation	Consumption of carcass	Predation (unconfirmed)	PCR analysis – no primer hits	Y	N
M11	Predation	Puncture wounds, northern goshawk present	Predation – avian spp.	Wounds consistent with avian predation	Y	N
M12	Vehicle strike	Carcass found along road, not consumed	Vehicle strike	Wounds consistent with blunt trauma, positive for brodifacoum (0.04 ppm)	N	Y
M13	Predation	Consumption of carcass	Predation – bobcat	PCR analysis – bobcat primer hits	Y	Y
M20	Predation	None	Predation (unconfirmed)	PCR analysis – no primer hits	Y	N
M21	Predation	Consumption of carcass	Predation – bobcat	PCR analysis – bobcat primer hits	Y	N
M40	Predation	Consumption of carcass	None	None	N	N
M43	Predation	Consumption of carcass	None	None	N	N

Thirteen marten mortalities were suspected to be the result of predation based on field assessments, of which 7 (54%) were confirmed as predation via molecular analysis. Five of these (71%) were confirmed as predation by bobcats, 1 was confirmed as a felid but could not be identified to species. We confirmed 1 as an avian predator, suspected to be a northern goshawk that we observed near the site of the dying marten, but we could not identify the predator to species with molecular data (Table 3). Three additional mortalities were caused by varied sources. One female marten was entrapped in a subnivean tunnel and died because of dehydration and resultant renal failure. This animal was presumed to have been entrapped by her collar during field assessment but exhibited adequate subcutaneous and visceral adipose stores, suggesting she was not entrapped long enough to experience starvation and that her collar did not cause her entrapment. One male marten had both bright red, fresh blood and dark, coagulated blood in his stomach with no associated gross or histological lesions. His liver tested positive for 2 second-generation anticoagulant rodenticides, brodifacoum (0.74 ppm) and difethialone (0.059 ppm), both of which are currently banned in California (California Legislative Assembly 2020). The death of this animal was ruled as anticoagulant rodenticide toxicosis, representing the first known instance of a marten mortality directly attributed to anticoagulant rodenticide exposure. A final male marten was found dead on a road, with the cause of death classified as blunt trauma from a presumed vehicle strike. This individual also tested positive for brodifacoum (0.04 ppm), but anticoagulant rodenticide exposure did not appear to contribute to mortality in this case. Thus, 2 out of the 5 martens necropsied tested positive for anticoagulant rodenticide exposure.

DISCUSSION

This study contributed to our understanding of factors influencing Pacific marten demography by estimating survival patterns, clarifying mortality sources, and identifying emerging threats. Annual marten survival estimates were relatively high compared to previous studies, although previous estimates have varied between populations and are bounded by uncertainty (Table 1). Monthly marten survival within this study system was lowest in the spring and summer month—specifically, April for females and July and August for males. During these periods, martens engage in sex-specific behaviors and reproductive processes that likely result in increased activity levels and energetic requirements for the respective sexes (Gittleman and Thompson 1988). Given female martens gestate for approximately 30 days and give birth in our study area from mid-April to mid-May (Delheimer et al. 2021), the timing of increased mortality in our research directly corresponded to when females would have been actively pregnant or lactating. This finding corroborates previous reports that female marten survival is lowest from pregnancy to weaning (Wilk and Raphael 2018), when females appear to be particularly susceptible to predation (Bull and Heater 2001). Similar patterns of survival have also been observed in closely related fishers; in a Minnesota fisher population, approximately 75% of females that were killed by predators were actively nursing or lactating when they died (Erb et al. 2014). Peaks in mortality of male martens in our study directly corresponded to the peak of mating season (Jul–Aug), when males may make exploratory or extra-territorial movements to access reproductively viable females. We posit decreased survival during these periods is a fitness cost incurred by the need to meet increased energetic requirements due to reproduction (e.g., parturition, lactation) and increased likelihood of encountering and succumbing to predators during increased foraging or reproduction-related activities (e.g., mate-seeking).

Though our study represents the second largest sample size used to estimate survival of an untrapped North American marten population, our survival estimates still exhibited some uncertainty and precluded our ability to robustly evaluate sex-specific, stage-specific (e.g., juvenile, sub-adult), or inter-annual survival patterns. We observed more mortalities in the first portion of our study (n = 13, 2009–2013) than the second (n = 3, 2015–2017), suggesting that short-term research or monitoring efforts do not effectively describe variation in demographic trends, such as survival. Predicting demography from short-term data is based on an assumption of constant conditions and violations of this assumption can strongly influence inferences of demographic trends (Fox and

Gurevitch 2000). Future efforts to evaluate population demographics, including survival, of rare or cryptic species may be improved by standardized protocols that increase consistency between studies, collaborative studies occurring over broader geographic or temporal scales, or meta-analyses of existing data (Facka and Moriarty 2017).

Predation was a prevalent source of mortality in our study population, and bobcats were responsible for most confirmed predation events. This corroborates previous research in the western United States, where bobcats are frequently suspected or confirmed sources of Pacific marten predation (Figure 1; Table S1). For example, preliminary evidence suggests most or all mortalities documented (*n* = 9) in a population of Humboldt martens (*M. c. humboldtensis*) in California were the result of bobcat predation (K. M. Slauson, USDA Forest Service, unpublished data). In 2 studies in Oregon, bobcats were suspected in 44% and 29% of Pacific marten predations, respectively (Bull and Heater 2001, Wilk and Raphael 2018), although predator identities were not confirmed by clinical or molecular analyses. Bull and Heater (2001) and Wilk and Raphael (2018) additionally identified raptors (25% and 17% of suspected predations, respectively) and coyotes (11% and 49% of suspected predations, respectively) as common marten predators. We observed only 1 avian predation in our study (Table 3) and we did not document or suspect predation by coyotes. Nonetheless, potential marten predators, including coyotes, cougars, and the recently reintroduced fisher (Facka 2016), commonly occur within this study area. Though we did not document any marten predations by these predators, they may contribute to marten mortalities over time.

Clinical assessments provided the opportunity to confirm marten mortality causes via necropsy, identify predators using molecular techniques, and examine the underlying pathology of marten tissues. In the absence of clinical assessments, factors contributing to morbidity or mortality are often unknown, which may lead practitioners to incorrectly presume causes of death (Gabriel et al. 2015). For example, our clinical assessments revealed that 2 martens were exposed to anticoagulant rodenticides, with coagulopathy due to toxicosis indicated as the cause of death for 1 individual. These observations would have been indeterminable during field-based assessments of mortality, underscoring the importance of evaluating proximate and ultimate causes of death with robust clinical techniques. Exposure to anticoagulant rodenticides, likely via consumption of poisoned prey, can directly result in wildlife mortality (Poessel et al. 2015), produce sub-lethal effects such as immune dysfunction (Riley et al. 2007, Serieys et al. 2018), and remain present in reproductive tracts to be passed on to gestating offspring (Gabriel et al. 2015, Wiens et al. 2019). The length of time that these toxicants persist in the environment after application is unclear (Van den Brink et al. 2018). For relatively short-lived species, such as martens, a persistent toxicant that can impart severe physiological consequences over multiple generations could have substantial deleterious effects. These consequences could be particularly dire for imperiled or at-risk populations, including the California state endangered and federally threatened coastal distinct population segment of Pacific martens (i.e., Humboldt marten; U.S. Fish and Wildlife Service 2020).

Though predation was a primary mortality source for martens, it is unclear whether observed survival patterns limit marten population growth in this area. If observed survival rates do lead to decreases in population size (e.g., via reduced reproductive success), then reducing predation risk could be considered to promote marten persistence. Direct predator removal is an ecologically improbable task that could result in undesirable outcomes including trophic cascades, net population increases of the removed predator, or increases in sympatric or co-occurring carnivores (Prugh et al. 2009, Estes et al. 2011). It may be possible, however, to indirectly mitigate predation risk for martens, other subordinate carnivores, or prey species by decreasing the foraging efficacy of predators (Vanlandeghem et al. 2021). At broad (Cushman et al. 2011, Zielinski 2014, Aylward et al. 2020) and fine scales (Tweedy et al. 2019), martens are generally associated with structurally heterogeneous forest cover and often avoid areas with reduced cover (Moriarty et al. 2016), rarely enter openings during snow-free periods (Moriarty et al. 2015, Martin et al. 2021), and exhibit increased movement rates and energetic expenditures in simplified forest stands (Moriarty et al. 2016, Martin et al. 2020). Presumably, martens avoid open or structurally homogeneous areas to reduce risk of predation or competition, yet no studies have empirically investigated the influence of forest structure on marten predation risk or encounters with competitors. Of few studies that have linked marten survival to forest structure, the primary source of marten mortality was trapping rather than predation (Thompson 1994, Johnson et al. 2009). Future studies that investigate the relationship between forest structure and marten survival may be able to link demographic outcomes to structural complexity and provide empirical guidance for forest management strategies that can positively influence marten persistence.

MANAGEMENT IMPLICATIONS

When combined, field-based and clinical assessments of mortality events provide ecologists and wildlife professionals the opportunity to elucidate the mechanisms that influence the health, survival, and demography of animal populations. While field assessments remain valuable, clinical methods provide more context and precision when evaluating proximate and ultimate causes of mortality. Further, clinical methods can elucidate physiological conditions (e.g., disease, starvation) or reveal unexpected outcomes (e.g., toxicant exposure) that may not be evident in the field. In particular, exposure to anticoagulant rodenticides may be a novel stressor for marten populations and whether marten exposure to anticoagulant rodenticides is a local or widespread concern is unknown. In future applications of clinical methods, we recommend frequent status checks on collared animals (i.e., every 1–3 days) and timely collection of carcasses to minimize scavenging and maximize ability to determine causes of mortality and morbidity. Collecting and testing tissue samples from animal carcasses, particularly from the liver, should be completed whenever possible to better understand the prevalence and effects of rodenticide exposure on wildlife populations. Concerted efforts to eliminate the use of toxicants, minimize exposure, and better understand the physiological effects of exposure will benefit human and wildlife health.

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CONFLICT OF INTERESTS

The authors declare that there are no conflicts of interest.

ETHICS STATEMENT

We adhered to protocols approved by the Institutional Animal Care and Use Committees of Oregon State University (3944, 4367) and USDA Forest Service (2015-002), maintained a current California Department of Fish and Scientific Collection Permit with a Memorandum of Understanding (SC-10793), and followed the American Society of Mammalogists' guidelines for the use of mammals in research (Sikes et al. 2016).

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SUPPORTING INFORMATION

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