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SURVIVAL AND PREDATORS OF PACIFIC MARTEN IN A SALVAGE-LOGGED PINE FOREST, SOUTH-CENTRAL OREGON

RANDALL J WILK AND MARTIN G RAPHAEL

ABSTRACT—Estimating marten (*Martes* spp.) survival rates in managed forests is important for comparisons with vital rates in unmanaged forests, and data across populations in different forest types are needed in meta-analyses. We estimated survival rates of a Pacific Marten (*Martes caurina*) population from 1993 to 1998. This population experienced no fur trapping and occurred in an atypical habitat of sparse tree-canopy cover, small tree diameters, and many natural openings and logging clearcuts. In the beetle-damaged, salvage-logged Lodgepole Pine (*Pinus contorta*) forest, downed wood and snags were removed and slash piles were accumulated to mitigate logging effects. The average annual probability of adult (≥ 1 y) survival was 0.684, $s_x = 0.104$ ($n = 53$). The overall adult survival did not differ between years or between the sexes across years. Average annual survival of young (< 1 y) was 0.753, $s_x = 0.118$ ($n = 26$). Seasonal survival of adults (0.945, $s_x = 0.027$) and young (0.974, $s_x = 0.026$) was highest in winter (December through February), and lowest in summer (June through August; adults = 0.853, $s_x = 0.035$; young = 0.902, $s_x = 0.046$). Adult winter survival was significantly greater than summer survival; and for adult females, winter survival was greater than in the other seasons (other seasons range = 0.862 to 0.903) and greater than male winter survival (0.918, $s_x = 0.039$), because there were no known female losses during the period (survival = 1.0). Based on evidence at field recovery sites and laboratory necropsies, predators were associated with 74% of all recovered marten carcasses, including Coyote (*Canis latrans*), Bobcat (*Lynx rufus*), American Badger (*Taxidea taxus*), and raptors of unknown species. Slash piles were used by marten, but the mitigation experiment was discontinued after logging. We suggest that slash piles may have helped sustain the local population of marten in the short term.

Keywords: *Dendroctonus ponderosae*, forest carnivore, Lodgepole Pine, *Martes caurina*, Mountain Pine Beetle, *Neotamias*, Pacific Northwest, *Pinus contorta*, slash piles, *Spermophilus*

Estimating marten (*Martes* spp.) survival rates in managed forests is important for comparisons with vital rates in unmanaged forests, and estimates from populations across different forest types are particularly useful in meta-analyses. In old conifer forests in the western

United States, marten use cavities in large-diameter trees and in ground-level stumps and logs for resting and denning (Buskirk and Zielinski 2003; Shirk and others 2014). Logging of marten habitat may negatively affect breeding, foraging, and predator avoidance behaviors. However, logging effects may be mitigated if forest stand complexity, cover, and physical structures near the ground are sufficiently managed to meet these requirements (Buskirk and Zielinski 2003; Bull and others 2005; Thompson and others 2012; Moriarty and others 2016a). For example, manipulated logging slash piles provided marten denning and resting sites (Raphael and Jones 1997). They also appear to be refugia for several species of small mammals, and thus prey reservoirs for marten. For example, in beetle-damaged Lodgepole Pine (*Pinus contorta*) forests in British Columbia, salvage logging with operational-scale-size slash piles or windrows in clearcuts enhanced abundance and species richness of the small-mammal community, allowed for the persistence of important prey species associated with closed-canopy forests, and dramatically ameliorated the negative effects observed in clearcuts without slash piles (Sullivan and others 2012). In our study area, the logged landscape provided habitat conditions highly suitable to ground-dwelling small mammals. We found that marten scats contained novel high frequencies of occurrence of vole-size and squirrel-size species and a relatively high year-round frequency of occurrence of the main prey, chipmunks (*Neotamias* spp.) and ground squirrels (*Spermophilus* spp.) (Wilk and Raphael 2017).

Pacific Marten (*Martes caurina*) mostly occur along the North Pacific Coast of North America (Moriarty and others 2016b; Dawson and others 2017). In central Oregon, the focus of this study, Mountain Pine Beetles (*Dendroctonus ponderosae*) regularly infest Lodgepole Pine forests that marten inhabit, which often results in salvage logging of affected areas. The magnitude of these outbreaks may be exacerbated by global warm-

ing (Kurz and others 2008; Braden 2011). Habitat in the area may be at the limit of marten adaptation owing to sparse canopy cover, small tree diameter, and numerous natural openings and logging clearcuts that marten generally avoid (Shirk and others 2014). In this regard, survival estimates will also contribute to understanding marten responses to these atypical environmental conditions.

Our analysis arose from a habitat mitigation experiment turned natural history study of Pacific Marten in an Oregon location and managed forest type where marten survival and predator information has not been previously reported. The study was originally planned to determine whether slash piles could mitigate negative effects from logging of marten habitat (Jones and others 1996). The experiment was discontinued after the planned pile configurations and volume goals were not achieved, resulting in low statistical power (Raphael and others 1996). Although marten fur trapping occurred in Oregon during the period, it was discouraged in the study area, and we are aware of no trapping mortality during the years we included in the current analysis (Jones and others 1996). Our research provides an important data point on natural survival rates where fur trapping does not occur (see Buskirk and others 2012). Our objective was to estimate the survival rates and predators of Pacific Marten and discuss the role of slash piles in the logged environment after comparing survival rates across the 6-y study period.

Our study was in an 85-km² area located on a pumice plateau at about 1700 m elevation in the Fremont-Winema National Forest, northeast of Chemult, Oregon, east of the Cascade Range crest. Forest cover was dominated by climax Lodgepole Pine-Bitterbrush shrub (*Purshia tridentata*), and higher hills supported Ponderosa Pine (*Pinus ponderosa*), Sugar Pine (*Pinus lambertiana*), Western White Pine (*Pinus monticola*), White Fir (*Abies concolor*), and Red Fir (*Abies magnifica*) (Franklin and Dyrness 1988). In addition to beetle-killed trees, the logging operation (1995–1996) removed downed woody debris and snags, and accumulated slash piles. Before logging (1993–1995) there were about 4.8 large and 10.7 small slash piles/km², and after logging (1996–1998), densities were >17.6/km² (Jones and Raphael 1990; Katnik and others 1994; Raphael and others 1998).

Marten were live-trapped year-round along forest roads and spurs using weather-proofed wire traps (Raphael and others 1993; Jones and others 1996; Raphael and Jones 1997). Marten were sedated and marked with lip tattoos and sequential small ear tags, chronologically, regardless of age or sex, and adults and yearlings were radio-collared (Telonics model MOD-70, Mesa, AZ). Kits were captured and ear-tagged at maternal dens. A maternal den is where kits are present exclusive of parturition and structures are used by females in rearing dependent young. These kits were radio-collared when re-captured at yearling-age or older. Marten were located about twice/wk year-round using triangulation from ground vehicles and by intermittent aerial tracking. Females were not disturbed during the parturition period.

We compiled weekly summaries from capture, marking, and telemetry-tracking field records over the period May 1993 through November 1998. We created a monthly survival timeline for the adult and young age classes determined at 1st capture and excluded individuals that were not assigned to an age class at that time. We classified marten as adults if we estimated them to be ≥ 1 y old and young if < 1 y old. Young included the kit cohort, in addition to those captured in spring that were marked as kits in the previous year (also referred to as juveniles in some studies). We used other field age indicators such as sagittal crest development, molar tooth wear, weight, and reproductive condition to refine age estimates (Raphael and others 1993; Jones and others 1996). The process enabled us to back-date and maintain continuous timelines of individuals that were marked but not collared when 1st captured but were later collared after recapture or were re-collared after collars were temporarily removed.

We used the assumption-free modified Kaplan-Meier estimator ($\hat{S}(t)$) that allows for censoring and for adding new individuals during the study (staggered entry). This enabled us to directly compare our results with published studies in northeastern (NE) Oregon (concurrent with our study; Bull and Heater 2001), and in northern Wisconsin (McCann and others 2010), using the same estimator as ours, and with predation as the primary known cause of marten mortalities.

We classified marten as either active (“at risk”, alive/tracked), dead, or censored. Censoring

occurred when contact with a known individual was lost in the study area from a collar malfunction or removal, or status was not known; for example, an animal that dispersed from the study area. We returned censored marten to the data set as active if they were later detected in the study area or were recaptured and/or recollared after being out of contact.

We calculated marten annual survival from the monthly entries for each year but excluded 2 trapping mortalities. We did not compute survival for the young male cohort, owing to small samples ($n \leq 4$ at risk each month), but we pooled young males into the estimates for total young female-male survival. We computed survival for 4 time periods or seasons in the calendar year (similar to a long-term study in Wisconsin), by pooling data across years for each season. The seasons were spring, March through May, which included the parturition (about 15 April to 15 May; Jones and others 1996; sometimes called natal denning) and maternal denning period (described above). Summer was June through August, which included the core post-natal denning and into the breeding period (Jones and Raphael 1995; Verts and Carraway 1998); autumn, September through November; and winter, December through February.

We graphed adult survival for each month through the 67-mo study period, and we present survival estimates in tables with standard errors (s_x) for use in meta-analyses by other researchers. We used the 95% confidence interval (CI) error bar overlap probability statistics to compare estimates, where overlap to about $\frac{1}{2} + (0.59)$ the length of an error bar is $P \approx 0.05$, and for the area between slight overlap of error bars to $\frac{1}{2}$ arm length is $P \leq 0.05$. If the error bars are slightly touching (≤ 0.14 overlap), $P = 0.01$. If the gap between arms is approximately $\frac{1}{3}$ the length of a single error bar (-0.37), $P \approx 0.001$, and if $> \frac{1}{3}$ the length of a single error bar, $P < 0.001$ (Cumming 2009). We show CIs only for significant results or results we believe were needed for specific comparisons. We used IBM SPSS Statistics v. 24 (IBM Corporation 2016) to process data and followed Pollock and others (1989) for survival estimates.

We evaluated the site evidence from recovered marten carcasses and identified predators from the field observations and by laboratory necropsy. Evidence of predators at the recovery site

TABLE 1. Age composition of radio collared-marked Pacific Marten at time of 1st capture (n , [%]) in south-central Oregon, 1993–1998.

Category	Pacific Marten n (%)		
	Female	Male	Total
Kit of the year ^a	11 (12.2)	9 (10.0)	20 (22.2)
Yearling (<1 y) ^a	3 (3.3)	3 (3.3)	6 (6.7)
Adult (≥ 1 y)	18 (20.0)	35 (38.9)	53 (58.9)
Subtotal	32 (35.6)	47 (52.2)	79 (87.8)
Not age classified ^b	4 (4.4)	7 (7.8)	11 (12.2)
Total	36 (40.0)	54 (54.6)	90 (100.0)

^a Groups were pooled into the <1 y category for analysis.

^b Not used in analysis.

included tracks, fur, feathers, scat, buried carcasses (Bobcats [*Lynx rufus*]; Bull and Heater 2001), as well as tooth marks in body tissue, body trauma (especially subcutaneous hemorrhage), or peeled-back skin, and partially consumed carcasses with skin picked clean from bones by raptors. These observations were supplemented by laboratory measurements of the width of inter-canine tooth marks in body tissue made by mammals (Bull and Heater 2001; McCann and others 2010). The evidence from carcasses alone was often insufficient to conclusively identify all predators or distinguish predation from scavenging.

In total, 115 marten were captured, but not all were collared or marked during the time of 1st capture. Of those that were, 79 were assigned to an age class for our analysis (Table 1). Across the study period, there was a monthly average of 14 adult and 7 young marten tracked, with as many as 19 adults and 15 young in a given month. On average, twice as many adult males were monitored as females, and more than 3 times as many young females were monitored as males.

Annual probability of survival of adult (0.684, $s_x = 0.104$, $n = 53$) and young marten (0.753, $s_x = 0.118$, $n = 26$) was not different (Table 2; Fig. 1). Overall adult survival did not differ across years or between the sexes across years. Young survival in the logging year (1996) was greater than the preceding year ($P < 0.05$; Table 2).

Seasonal probability of survival of adult marten was highest in winter (December through February; 0.945, $s_x = 0.027$) and lowest in summer (June through August; 0.853, $s_x = 0.035$) and differed between the 2 seasons ($P < 0.05$) (Table 3). Adult female winter survival was greater than adult female spring survival (March through

TABLE 2. Annual probability of Pacific Marten adult-young survival (Kaplan-Meier $\hat{S}(t)$, $s_{\bar{x}}$) from monthly entries for each year. Estimates for young males were not computed owing to small samples, but numbers were incorporated in the total for young.

	Young $\hat{S}(t)$ ($s_{\bar{x}}$)		Adult $\hat{S}(t)$ (s)		
	Female	Total	Female	Male	Total
1993	—	—	0.500 (0.250)	0.728 (0.102)	0.680 (0.096)
1994	—	—	0.556 (0.151)	0.469 (0.129)	0.536 (0.101)
1995	0.750 (0.188)	0.556 (0.117)	0.833 (0.170)	0.729 (0.155)	0.779 (0.116)
1996	0.750 (0.119)	0.875 (0.086)*	0.625 (0.156)	0.622 (0.128)	0.621 (0.099)
1997	0.909 (0.079)	0.743 (0.105)	0.667 (0.157)	0.720 (0.106)	0.725 (0.087)
1998	0.825 (0.173)	0.839 (0.168)	0.833 (0.196)	0.733 (0.155)	0.763 (0.124)
Mean	0.809 (0.140)	0.753 (0.118)	0.669 (0.180)	0.667 (0.129)	0.684 (0.104)

* Significantly different (CI = 0.706–1.044) from preceding year (CI = 0.327–0.785) ($P < 0.05$).

May; 0.862, $s_{\bar{x}} = 0.059$) and greater than adult male winter survival (0.918, $s_{\bar{x}} = 0.039$) (both $P < 0.01$) because there were no known female losses during the period ($\hat{S}(t) = 1$; Table 3).

We estimated that predators either killed, scavenged, or visited marten carcasses in 74% of the recovered mortalities. Most of the 47 apparent natural deaths occurred in May and June (34.0%), and 94% of those were caused by or were scavenged by predators. Only 14.9% of mortalities occurred between December and April, and no known predation-scavenging on marten was recorded for the months of December and January. Starvation, hypothermia, or poisoning was suspected in 2 deaths (1 of these was

recovered from a cabin; see Holyan and others 1998), and 9 other causes were not known.

Of the 35 marten likely killed by predators, 15 were females and 20 were males. Specifically, 28 marten showed evidence of mammalian presence (80.0% of predator associations) and 6 of raptor presence (17.1%). Puncture-wound canine-width measurements and tracks confirmed the presence of Coyotes (*Canis latrans*), Bobcats, and American Badgers (*Taxidea taxus*) at recovered marten carcasses. Coyotes were estimated to be associated with 10 marten carcasses, and possibly as many as 17, Bobcats with 4, and as many as 10, and American Badgers with 1, and as many as 4. One badger was actually captured

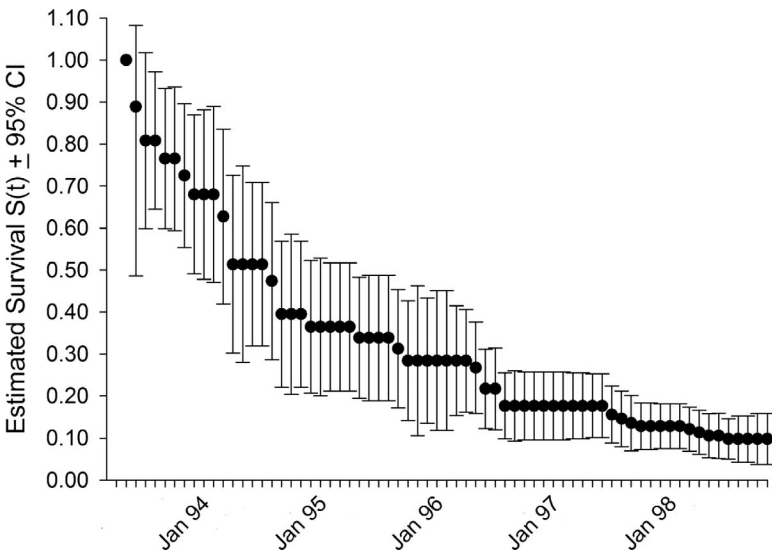


FIGURE 1. Decremental survival (Kaplan-Meier $\hat{S}(t)$, 95% confidence interval) calculated at 1-mo intervals across 67 mo for adult Pacific Marten (≥ 1 y-old; $n = 53$) in south-central Oregon, May 1993 through November 1998.

TABLE 3. Season-specific (pooled across years) probability of survival (Kaplan-Meier $\hat{S}(t)$, $s_{\hat{x}}$) of Pacific Marten in south-central Oregon, 1993–1998.

Season	Young $\hat{S}(t)$ ($s_{\hat{x}}$)			Adult $\hat{S}(t)$ ($s_{\hat{x}}$)		
	Female	Male	Total	Female	Male	Total
Mar–May ^a	0.962 (0.035)	0.800 (0.119)	0.917 (0.043)	0.862 (0.059)	0.917 (0.037)	0.898 (0.032)
Jun–Aug	0.936 (0.044)	0.800 (0.119)	0.902 (0.046)	0.903 (0.052)	0.827 (0.045)	0.853 (0.035)
Sep–Nov	0.936 (0.041)	0.857 (0.102)	0.920 (0.040)	0.894 (0.058)	0.911 (0.037)	0.905 (0.031)
Dec–Feb	0.964 (0.034)	1.000 (0.0)	0.974 (0.026)	1.000 (0.0)*	0.918 (0.039)	0.945 (0.027) †

^a Mar–May = spring, Jun–Aug = summer, Sep–Nov = autumn, Dec–Feb = winter.

* Greater than Mar–May (Mar–May CI = 0.747–0.976; also > adult male Dec–Feb: CI = 0.843–0.994; both $P < 0.01$).

† Greater than Jun–Aug (CI = 0.893–0.997; Jun–Aug CI = 0.784–0.922, $P < 0.05$).

and released alive from a marten trap near the end of the study.

Adult survival in our study was in the middle range of survival estimates for sexes combined and for females, and in the low-middle range for males across studies in the marten range (Table 4). CIs around closely grouped point estimates in the table would likely reveal no differences between/among them. The NE Oregon study was concurrent with 4 y of our study, but it grouped juveniles that were ≥ 9 -mo old with adults, and computations were for 2-mo intervals (Bull and Heater 2001). In that Lodgepole Pine-Grand Fir (*Abies grandis*)-Douglas-fir (*Pseudotsuga menziesii*) landscape, the average of the annual survival point estimate was 0.63, CI = 0.59 to 0.67, not different from the concurrent period with our study, 0.665, CI = 0.61 to 0.72.

There were few published studies related to survival of young, particularly in populations without active fur trapping, and none were directly comparable to our study, based upon average annual survival (Table 2). For example, over a 2.5-y study in an intensively trapped population (90% of the losses) in Maine, Hodgman and others (1994) estimated survival rates of juvenile females (< 1 y) at 1.00 for the interval 1 September to 31 October, 0.20 for 1 to 14 November (1st 2 wk of trapping season), and 1.00 for 15 November to 15 December (last 4 wk of season) ($n = 12$). Juvenile male survival was 0.82, 0.11, and 1.00 over the same periods, respectively ($n = 12$). In cut and uncut forests combined with fur trapping in western Quebec, dispersing male survival was 0.21/y (Potvin and Breton 1997). Another study of dispersing juveniles in the boreal forest in Ontario showed that 60% of the losses were from trapping (Johnson and others 2009).

Our adult female survival of 0.78, CI = 0.65 to 0.91 during the consecutive 2-season spring-

summer natal and post-natal denning periods was not different from the “kit-rearing” time period (16 March to 15 July) in a long-term study in northern Wisconsin (0.92, CI = 0.80 to 1.04; McCann and others 2010). However, for adult males over the same periods, estimated survival in our study (0.76, CI = 0.66 to 0.86) was lower than in Wisconsin (0.93, CI = 0.83 to 1.03; $P < 0.05$). Estimated survival during the summer–autumn (16 July to 15 November) period in the Wisconsin study (both sexes = 1.00, CI = 1.00 to 1.00) also exceeded the summer–autumn (June through November) period in our study (females: 0.81, CI = 0.67 to 0.95 [$P < 0.01$]; males: 0.75, CI = 0.65 to 0.85 [$P < 0.001$]), respectively. Conversely, female winter survival in our study (December through February; 1.00, CI = 1.00 to 1.00) exceeded that of females in northern Wisconsin (16 November to 15 March; 0.83, 0.69 to 0.97; $P < 0.01$), but our adult male winter survival (0.92, CI = 0.84 to 0.99) did not differ from Wisconsin (0.91, CI = 0.81 to 1.01).

Most of the recovered marten carcasses in our study showed evidence of predation by Coyotes, Bobcats, and American Badgers. Unfortunately, in several cases the forensic techniques could not determine with certainty all species, and whether marten were killed or scavenged. Improved current techniques allow for predator DNA in saliva left on carcasses to definitively identify canid and felid predator species (Wengert and others 2013), but predation or scavenging are still uncertain. Our confirmation of 1 American Badger kill was done by comparing a badger skull with tooth puncture wounds in the marten. This may be the 1st report of American Badger as a predator of marten (at least in this region). Both species seem to have the same prey base, particularly ground squirrels (Messick and Hornocker 1981; Wilk and Raphael 2017). Note that

TABLE 4. Annual adult marten survival estimates since 1994 (McCann and others 2010: Table 4; Buskirk and others 2012: Table 5.1) with 2 subsequent additions (denoted with *).

Source	Location	Study area	Marten trapping ^a	Survival
BOTH SEXES ADULTS				
Thompson (1994)	Ontario, Canada	Uncut forest	Yes	0.91 ^b
McCann and others (2010)	Northern Wisconsin	Cut/uncut forest	No	0.81
Current study*	South-central Oregon	Pre/post-logged forest	No	0.68 ^d
Bull and Heater (2001)	Northeastern Oregon	Uncut forest	No	0.63
Thompson (1994)	Ontario, Canada	Logged forest	Yes	0.63 ^b
Moriarty (2014)*	Northern California	Cut/uncut forest	No	0.63 ^c
FEMALE ADULTS				
Hearn (2007)	Newfoundland, Canada	In/out-side reserve	No	0.83
Payer (1999)	Maine	Industrial forest	No	0.81
McCann and others (2010)	Northern Wisconsin	Cut/uncut forest	No	0.77
Current study*	South-central Oregon	Pre/post-logged forest	No	0.67 ^d
Payer and Harrison (1999)	Maine	Industrial forest	Yes	0.66
Moriarty (2014)*	Northern California	Cut/uncut forest	No	0.64 ^c
Payer and Harrison (1999)	Maine	Forest reserve	No	0.62
Hodgman and others (1997)	Maine	Forest reserve	No	0.53
MALE ADULTS				
Payer and Harrison (1999)	Maine	Forest reserve	No	0.95
Hodgman and others (1997)	Maine	Forest reserve	No	0.87
McCann and others (2010)	Northern Wisconsin	Cut/uncut forest	No	0.85
Payer and Harrison (1999)	Maine	Industrial forest	No	0.84
Hearn (2007)	Newfoundland, Canada	In/out-side reserve	No	0.83
Potvin and Breton (1997)	Quebec, Canada	Uncut forest	Yes	0.69 ^d
Current study*	South-central Oregon	Pre/post-logged forest	No	0.67 ^d
Potvin and Breton (1997)	Quebec, Canada	Logged forest	No	0.62 ^d
Moriarty (2014)*	Northern California	Cut/uncut forest	No	0.61 ^c
Payer and Harrison (1999)	Maine	Industrial forest	Yes	0.51

^a Legal trapping during study. Our study occurred during legal seasons, but there was no evidence of trapping mortality.

^b Calculated from daily natural mortality during all years.

^c Calculated from daily mortality for adults.

^d Natural mortality only.

in our study area, we found American Badger in 1.1% of marten scats (Wilk and Raphael 2017).

In the NE Oregon study, Bobcats were the primary predator on marten (44% of the losses by predators) and Coyotes represented 11% of 18 kills assigned to predators; Northern Goshawks (*Accipiter gentilis*) were also implicated as predators (Bull and Heater 2001). In the Lassen National Forest in NE California, Bobcats also appeared to be the primary predator of marten (Moriarty and others 2014). In northern Wisconsin, Fishers (*Martes pennanti*) and raptors were the main predators (McCann and others 2010), as were Red Foxes (*Vulpes vulpes*) and Great Horned Owls (*Bubo virginianus*) in Ontario, Canada (Thompson 1994). In Maine, Coyotes, Fishers, raptors, and marten were identified as predators (Hodgman and others 1997). Cannibalism in marten is rare but was reported in NE Oregon (Bull and Heater 1995) and in Ontario (Thompson and Colgan 1987). In the latter study, it was not certain if losses were from killing or from scavenging during a period of food shortage.

We found significantly higher adult winter survival than summer survival, which was consistent with low incidence of marten losses during winter. The NE Oregon study also reported low winter predation losses of marten, which may be uncommon (Bull and Heater 2001). Reasons for low winter predation in our study may be related to reduced marten activity during daylight hours and more use of subnivean rest sites (Raphael and Jones 1997; Bull and Heater 2000, 2001), which lowers the risk of being observed by a predator during daylight compared to nighttime. Subnivean rest sites may be of high value in places where other potential tree rest sites are limited, as in our study, and contribute thermal benefits to marten in winter (Buskirk and others 1989; Bull and Heater 2000), which enhance survival. Prior to logging, Raphael and Jones (1997) recorded that 76% of marten resting-site radio locations in winter were subnivean. Reasons for higher winter predation on marten in other studies may be related to increased vulnerability from the lack

of cover in deciduous forests or from prey shortages (Bull and Heater 2001), both of which contribute to more foraging effort, energy demand, and predation risk. We are not certain why young survival was greater in our study in the logging year than in the preceding year, except that human presence was a factor between years.

Telemetry and camera monitoring of marten in our study area revealed high use of slash piles for denning and resting sites (Jones and others 1997; Raphael and Jones 1997; Raphael and others 1998). Studies have demonstrated the benefits of slash piles and wood debris to marten in helping to retain ground-level structure similar to older forests (Baker 1992; Payer and Harrison 2004), facilitate movement in cut forest (Moriarty and others 2016a), provide potential natal and maternal dens (Raphael and Jones 1997; Bull and Heater 2000), offer winter thermal cover (Buskirk and others 1989; Bull and Heater 2000), and maintain or increase prey availability (Payer and Harrison 2004; Wilk and Raphael 2017). In addition, concentrated sources of prey such as those found in and around piled slash may elevate prey availability, which in turn could enhance fitness and reproduction. Indeed, predation efficiency of marten on small mammals has been linked to higher abundances of coarse woody debris (Andruskiw and others 2008). Furthermore, chipmunks and ground squirrels, which had the highest frequencies of occurrence year-round in our study area, may have body sizes closest to meeting the optimal daily energy needs of marten (Slauson and Zielinski 2017). Such efficiency would enhance survival by reducing the energy demand for hunting and by reducing marten vulnerability to predation that would occur when hunting several smaller prey.

In our study area, slash piles were mostly used for denning, often with females using multiple den sites (Raphael and others 1998). Ample availability of slash-pile dens would help to enhance survival of young, especially females, which would ultimately increase fecundity and contribute to stable survival rates. In contrast to our study, slash piles in predominantly unmanaged mixed forests surrounded by extensively logged fragmented forest of NE Oregon were used only 7 and 6% of the time for resting and denning, respectively, based on radio locations, but pile densities were not reported (Bull and

Heater 2000), and they were not experimentally manipulated as in our study.

We found that marten used slash piles for denning and rest sites more than any other ground-level structure, that the study area provided a sustained marten prey abundance (Raphael and others 1998; Wilk and Raphael 2017), and that overall marten survivorship did not detectably decline. We speculate that slash piles may have served as a short-term habitat mitigation function. Other factors likely contributed, such as reduced fur trapping, or some other “beneficial” aspect of the forest environment after salvage logging. Slash piles do not replace natural den features such as logs, snags, rock crevices, and squirrel (*Tamiasciurus* spp.) middens (see Ruggiero and others 1998), but where logging occurs in pine forests, quantities of slash equal to or greater than those created during operational scale salvage logging may be a practical, important habitat management approach for maintaining ground-level structure and providing prey reservoirs for marten in south-central Oregon (see Sullivan and others 2012; Wilk and Raphael 2017). Highly variable configurations of slash piles described as artificially constructed multilayered stacks of branches and foliage, logs, ordered log decks for firewood cutting, stumps, and other debris ≥ 4 m² in ground-level surface area, with a minimum density of >18 piles/km² may be beneficial to Pacific Marten in the short term following salvage logging of the Lodgepole Pine forest in the region (Wilk and Raphael 2017).

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LITERATURE CITED

- ANDRUSKIW M, FRYXELL JM, THOMPSON ID, BAKER JA. 2008. Habitat-mediated variation in predation risk by the American Marten. *Ecology* 89:2273–2280.

- BAKER JM. 1992. Habitat use and spatial organization of Pine Marten on southern Vancouver Island, British Columbia [thesis]. Burnaby, BC: Simon Fraser University. 119 p.
- BRADEN G. 2011. Living on the edge: Surviving the tipping points of change. In: Braden G. Deep truth. Igniting the memory of our origin, history, destiny, and fate. Carlsbad, CA: Hay House. p 49–91.
- BULL EL, HEATER TW. 1995. Intraspecific predation on American Marten. *Northwestern Naturalist* 76:132–134.
- BULL EL, HEATER TW. 2000. Resting and denning sites of American Marten in northeastern Oregon. *Northwest Science* 74:179–185.
- BULL EL, HEATER TW. 2001. Survival, causes of mortality, and reproduction in the American Marten in northeastern Oregon. *Northwestern Naturalist* 82:1–6.
- BULL EL, HEATER TW, SHEPHERD JF. 2005. Habitat selection by American Marten in northeastern Oregon. *Northwest Science* 79:37–43.
- BUSKIRK SW, BOWMAN J, GILBERT JH. 2012. Population biology and matrix demographic modeling of American Martens and Fishers. In: Aubry KB, Zielinski WJ, Raphael MG, Proulx G, Buskirk SW, editors. *Biology and conservation of Marten, Sables, and Fishers, a new synthesis*. Ithaca, NY: Cornell University Press. p 77–92.
- BUSKIRK SW, FORREST FC, RAPHAEL MG, HARLOW HJ. 1989. Winter resting site ecology of marten in the central Rocky Mountains. *Journal of Wildlife Management* 53:191–196.
- BUSKIRK SW, ZIELINSKI WJ. 2003. Small and mid-sized carnivores. In: Zabel CJ, Anthony RG, editors. *Mammal community dynamics, management and conservation in the coniferous forests of western North America*. Cambridge, UK: Cambridge University Press. p 207–249.
- CUMMING G. 2009. Inference by eye: Reading the overlap of independent confidence intervals. *Statistics in Medicine* 28:205–220.
- DAWSON NG, COLELLA JP, SMALL MP, STONE KD, TALBOT SL, COOK JA. 2017. Historical biogeography sets the foundation for contemporary conservation of martens (genus *Martes*) in northwestern North America. *Journal of Mammalogy* 98:715–730.
- FRANKLIN JF, DYRNES CT. 1988. *Natural vegetation of Oregon and Washington*. Corvallis, OR: Oregon State University Press. 452 p.
- HEARN BJ. 2007. Factors affecting habitat selection and population characteristics of American Marten (*Martes americana*) in Newfoundland [dissertation]. Orono, ME: University of Maine.
- HODGMAN TP, HARRISON DJ, KATNIK DD, ELOWE KD. 1994. Survival in an intensively trapped marten population in Maine. *Journal of Wildlife Management* 58:593–600.
- HODGMAN TP, HARRISON DJ, PHILLIPS DM, ELOWE KD. 1997. Survival of American Marten in an untrapped forest preserve in Maine. In: Proulx G, Bryant HN, Woodward PM, editors. *Martes: Taxonomy, ecology, techniques, and management*. Edmonton, AB: Provincial Museum of Alberta. p 86–99.
- IBM CORPORATION. 2016. IBM SPSS. Statistics for Windows, version 24.0. Armonk, NY: IBM Corporation.
- JOHNSON CA, FRYXELL JM, THOMPSON ID, BAKER JA. 2009. Mortality risk increases with natal dispersal distance in American Marten. *Proceedings of the Royal Society B* 276:3361–3367.
- *JONES LLC, RAPHAEL MG. 1990. Marten ecology and management in fragmented habitats of the Pacific Northwest. Olympia, WA: US Department of Agriculture, Forest Service, Pacific Northwest Research Station. 44 p. Available from US Forest Service, Pacific Northwest Research Station, Forestry Sciences Laboratory, 3625 93rd Avenue SW, Olympia, WA 98512.
- *JONES LLC, RAPHAEL MG. 1995. Natural history and habitat use by American Marten in a central Oregon Lodgepole Pine ecosystem. Olympia, WA: US Department of Agriculture, Forest Service. 16 p. Available from US Forest Service, Pacific Northwest Research Station, Forestry Sciences Laboratory, 3625 93rd Avenue SW, Olympia, WA 98512.
- *JONES LLC, RAPHAEL MG, IRWIN LL. 1996. Ecology and management of American Marten in a Lodgepole Pine ecosystem in central Oregon. Olympia, WA: US Department of Agriculture, Forest Service. 36 p. Available from US Forest Service, Pacific Northwest Research Station, Forestry Sciences Laboratory, 3625 93rd Avenue SW, Olympia, WA 98512.
- JONES LLC, RAPHAEL MG, FORBES JT, CLARK LA. 1997. Using remotely activated cameras to monitor maternal dens of martens. In: Proulx G, Bryant HN, Woodward PM, editors. *Martes: Taxonomy, techniques, and management*. Edmonton, AB: The Provincial Museum of Alberta. p 329–349.
- KATNIK DD, HARRISON DJ, HODGMAN TP. 1994. Spatial relations in a harvested population of marten in Maine. *Journal of Wildlife Management* 58:600–607.
- KURZ WA, DYMOND CC, STINSON G, RAMPLEY GJ, NELSON ET, CARROLL AL, EBATA T, SAFRANYIK L. 2008. Mountain Pine Beetle and forest carbon feedback to climate change. *Nature* 452:987–990.
- McCANN NP, ZOLLNER PA, GILBERT JH. 2010. Survival of adult marten in northern Wisconsin. *Journal of Wildlife Management* 74:1502–1507.
- MESSICK JP, HORNOCKER MG. 1981. Ecology of the Badger in southwestern Idaho. *Wildlife Monographs* 76:1–52.

* Unpublished.

- *MORIARTY KM, EPPS CW, ZIELINSKI WJ. 2014. Pacific Marten (*Martes caurina*) habitat use and movement in Lassen National Forest, California. Arcata, CA: US Department of Agriculture, Forest Service. 148 p. Available from US Forest Service, Pacific Southwest Research Station, Redwood Sciences Laboratory, Arcata, CA.
- MORIARTY KM, EPPS CW, ZIELINSKI WJ. 2016a. Forest thinning changes movement patterns and habitat use by Pacific Marten. *Journal of Wildlife Management* 80:621–633.
- MORIARTY KM, BAILEY JD, SMYTHE SE, VERSCHUYL J. 2016b. Distribution of Pacific Marten in coastal Oregon. *Northwestern Naturalist* 97:71–81.
- PAYER DC. 1999. Influences of timber harvesting and trapping on habitat selection and demographic characteristics of marten [dissertation]. Orono, ME: University of Maine.
- *PAYER D, HARRISON D. 1999. Influences of timber harvesting and trapping on habitat selection and demographic characteristics of marten. Orono, ME: University of Maine Cooperative Forestry Research Unit.
- PAYER D, HARRISON D. 2004. Relationships between forest structure and habitat use by American Marten in Maine, USA. In: Harrison DJ, Fuller AK, Proulx G, editors. *Marten and Fishers (Martes)* in human-altered environments, an international perspective. New York, NY: Springer Science+Business Media, Inc. p 173–186.
- POLLOCK KH, WINTERSTEIN SR, BUNK CM, CURTIS PD. 1989. Survival analysis in telemetry studies: The staggered entry design. *Journal of Wildlife Management* 53:7–15.
- POTVIN F, BRETON L. 1997. Short-term effects of clearcutting on marten and their prey in the boreal forest of western Quebec. In: Proulx G, Bryant HN, Woodard PM, editors. *Martes: Taxonomy, techniques, and management*. Edmonton, AB: The Provincial Museum of Alberta. p 452–474.
- RAPHAEL MG, JONES LLC. 1997. Characteristics of resting and denning sites of American Marten in central Oregon and western Washington. In: Proulx G, Bryant HN, Woodard PM, editors. *Martes: Taxonomy, techniques, and management*. Edmonton, AB: The Provincial Museum of Alberta. p 146–165.
- *RAPHAEL MG, IRWIN L, JONES LLC, CLARK LA, FORBES JT, SIMPSON T. 1993. Chemult marten study. Olympia, WA: US Department of Agriculture, Forest Service. 4 p. Available from US Forest Service, Pacific Northwest Research Station, Forestry Sciences Laboratory, 3625 93rd Avenue SW, Olympia, WA 98512.
- *RAPHAEL MG, JONES LLC, KATNIK D, CLARK L, HOYLAN J, DENNIS M, BREWSTER P, IRWIN L. 1996. Natural history and habitat use by American Marten in a central Oregon Lodgepole Pine ecosystem. Olympia, WA: US Department of Agriculture, Forest Service. 6 p. Available from US Forest Service, Pacific Northwest Research Station, Forestry Sciences Laboratory, 3625 93rd Avenue SW, Olympia, WA 98512.
- *RAPHAEL MG, JONES LLC, CLARK L, DENNIS M, HOYLAN J, IRWIN, L. 1998. Natural history and habitat use by American Marten in a central Oregon Lodgepole Pine ecosystem. Olympia, WA: US Department of Agriculture, Forest Service. 2 p. Available from US Forest Service, Pacific Northwest Research Station, Forestry Sciences Laboratory, 3625 93rd Avenue SW, Olympia, WA 98512.
- RUGGIERO LF, PEARSON DD, HENRY SE. 1998. Characteristics of American Marten den sites in Wyoming. *Journal of Wildlife Management* 62:663–673.
- SHIRK AJ, RAPHAEL MG, CUSHMAN SA. 2014. Spatiotemporal variation in resource selection: Insights from the American Marten (*Martes americana*). *Ecological Applications* 24:1434–1444.
- SLAUSON KM, ZIELINSKI WJ. 2017. Seasonal specialization in diet of the Humboldt Marten (*Martes caurina humboldtensis*) in California and the importance of prey size. *Journal of Mammalogy* 98:1697–1708. DOI: 10.1093/jmammal/gyx118.
- SULLIVAN TP, SULLIVAN DS, LINDGREN PMF, RANSOME B. 2012. If we build habitat, will they come? Woody debris structures and conservation of forest mammals. *Journal of Mammalogy* 93:1456–1468.
- THOMPSON I. 1994. Marten populations in uncut and logged boreal forests in Ontario. *Journal of Wildlife Management* 58:272–280.
- THOMPSON ID, COLGAN PW. 1987. Numerical responses of martens to a food shortage in northcentral Ontario. *Journal of Wildlife Management* 51:824–835.
- THOMPSON ID, FRYXELL J, HARRISON DJ. 2012. Improved insights into use of habitat by American Marten. In: Aubry KB, Zielinski WJ, Raphael MG, Proulx G, Buskirk SW, editors. *Biology and conservation of Marten, Sables and Fishers, a new synthesis*. Ithaca, NY: Cornell University Press. p 209–230.
- VERTS BJ, CARRAWAY N. 1998. Land mammals of Oregon. Berkeley, CA: University of California Press. 668 p.
- WENGERT GM, GABRIEL MW, FOLEY JE, KUN T, SACKS BN. 2013. Molecular techniques for identifying intra-guild predators of Fishers and other North American small carnivores. *Wildlife Society Bulletin* 37:659–663.
- WILK RJ, RAPHAEL MG. 2017. Food habits of Pacific Marten from scats in south-central Oregon. *Northwestern Naturalist* 98:243–250.

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