

Matthew S. Delheimer^{1, 2}, USDA Forest Service, Pacific Northwest Research Station, Corvallis Forestry Sciences Laboratory, 3200 SW Jefferson Way, Corvallis, Oregon 97331

Katie M. Moriarty³, USDA Forest Service, Pacific Northwest Research Station, Olympia Forestry Sciences Laboratory, 3625 93rd Avenue SW, Olympia, Washington 98512

Keith M. Slauson⁴, USDA Forest Service, Pacific Southwest Research Station, Redwood Sciences Laboratory, 1700 Bayview Drive, Arcata, California 95521

Alyssa M. Roddy⁵, USDA Forest Service, Pacific Northwest Research Station, Olympia Forestry Sciences Laboratory, 3625 93rd Avenue SW, Olympia, Washington 98512

and

Desiree A. Early and **Keith A. Hamm**, Green Diamond Resource Company, PO Box 68, Korb, California 95550

Comparative Reproductive Ecology of Two Subspecies of Pacific Marten (*Martes caurina*) in California

Abstract

Accurate information on reproductive ecology is necessary to develop conservation actions for at-risk wildlife species. Our objective was to describe female reproductive parameters and den use of two subspecies of wild, untrapped Pacific martens (Humboldt marten, *Martes caurina humboldtensis*; Sierran marten, *M. c. sierrae*) of conservation interest in California. We used radio telemetry and remotely triggered cameras to monitor 10 Humboldt martens (2014 to 2016) and six Sierran martens (2016 to 2017) over 23 total denning periods. For Humboldt martens, mean parturition date was 13 April, proportion of adult females reproducing was 80% ($n = 12$ of 15), and mean litter size was 1.8 ± 0.6 kits ($\bar{x} \pm SD$). For Sierran martens, mean parturition date was 29 April, proportion of adult females reproducing was 87% ($n = 7$ of 8), and mean litter size was 1.9 ± 0.7 kits. Humboldt and Sierran marten dens were predominantly located in woody structures, with live trees, snags, and logs comprising 91% and 79% of dens, respectively. Although reproductive ecologies of Humboldt and Sierran martens were largely similar, Sierran marten parturition dates were significantly later. We compare our study populations to other North American marten populations and examine factors that could influence consistency or variability in reproductive parameters between populations.

Keywords: Pacific marten, mustelid, reproduction, denning

Introduction

Accurate information on reproductive ecology is necessary to assess population dynamics and

develop appropriate conservation actions for at-risk wildlife species. A lack of information can result in disturbance to females and their offspring during critical periods of the reproductive cycle, a misunderstanding of reproductive potential and corresponding population trends, and degradation or loss of resources important to supporting reproduction (Hernandez et al. 2006, French et al. 2011, Barding and Lacki 2014). In the absence of local information, data on reproductive ecology from elsewhere within a species' geographic range or from closely related species may be used as a proxy. However, geographic locations can vary widely in abiotic conditions such as temperature and precipitation, which in turn can affect biotic conditions such as resource abundance or vegeta-

¹ Author to whom correspondence should be addressed.
Email: mattdelheimer@gmail.com

² Current address: USDA Forest Service, Pacific Southwest Research Station, Institute of Forest Genetics, 2480 Carson Road, Placerville, California 95667

³ Current address: National Council for Air and Stream Improvement, Inc., 227 NW 3rd Street, Corvallis, Oregon 97330

⁴ Current address: California Department of Parks and Recreation, PO Box 2006, Eureka, California 95502

⁵ Current address: Green Diamond Resource Company, PO Box 68, Korb, California 95550

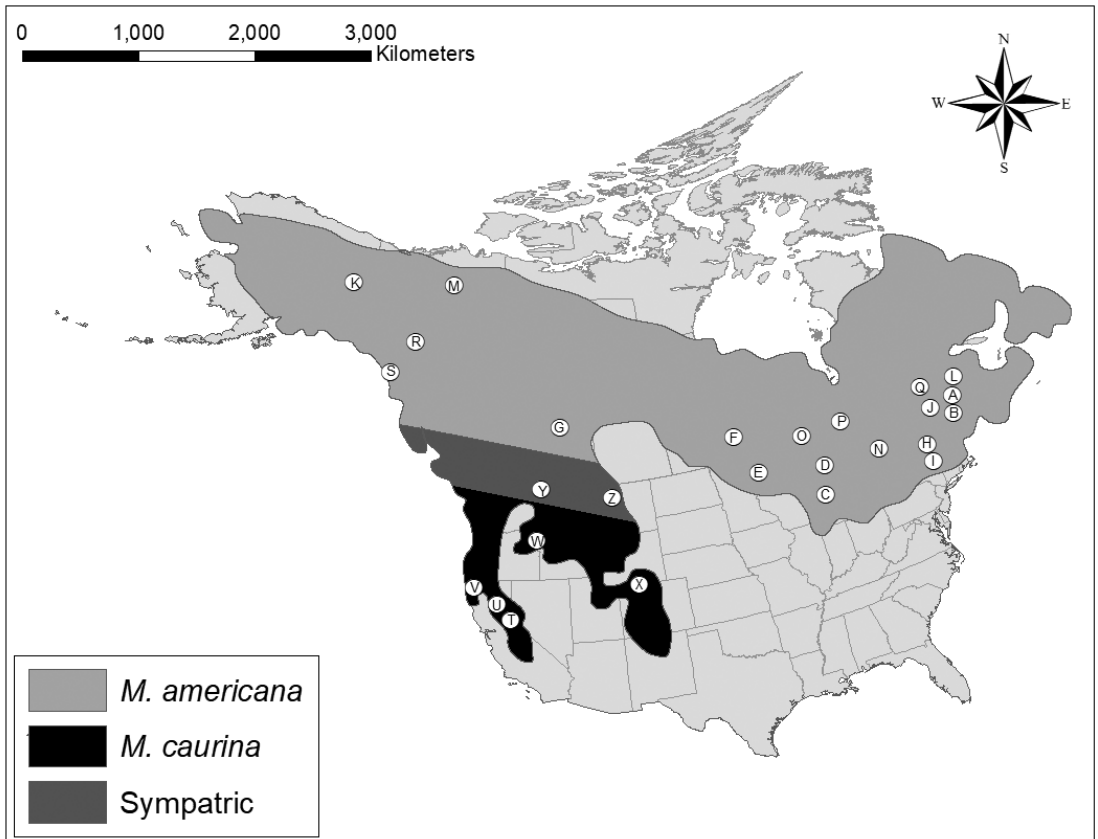


Figure 1. American marten (*Martes americana*) and Pacific marten (*M. caurina*) distributions in North America (adapted from Dawson et al. 2017), including a zone of potential sympatry and hybridization between American and Pacific martens (“Sympatric”). Geographic locations of the Humboldt marten (V; *M. c. humboldtensis*) and Sierran marten (U; *M. c. sierrae*) study areas in California and 24 previous studies examined for reproductive parameters of North American marten populations are indicated by a letter that corresponds with ID in Table 2.

tion communities (Bywater et al. 2010, Lada et al. 2013). While reproductive physiology (e.g., length of gestation) should be consistent across a species’ range, aspects of reproductive ecology (e.g., number of offspring produced) that can potentially be influenced by abiotic or biotic conditions may not be as generalizable. Comparison of local information to more broadly collected data may reveal where reproductive ecologies are consistent or divergent and whether generalization is appropriate.

Holarctic martens are forest-dependent mustelids that exhibit similar reproductive physiologies (Mead 1994, Green et al. 2017, Proulx and Aubry 2017), and include American and Pacific martens

(*Martes americana*, *M. caurina*) in North America, pine and stone martens (*M. martes*, *M. foinea*) in Asia and Europe, and Japanese martens and sables (*M. melampus*, *M. zibellina*) in Asia (Anderson 1970). American martens have a widespread distribution across the northern United States and Canada and occur across a broad range of latitudes (Figure 1; Dawson et al. 2017). Pacific martens have recently been recognized as a distinct species from the American marten (Dawson and Cook 2012, Dawson et al. 2017, Colella et al. 2018), although a zone of sympatry and hybridization exists (Figure 1). Pacific martens have a comparatively limited distribution along the Pacific Coast of the United States and Canada, with disjunct populations in the southern Rocky Mountains

and some Alaskan islands (Figure 1; Dawson et al. 2017). Much of the information concerning the reproductive ecology of North American martens has been garnered from studies of American marten populations (Green et al. 2017).

There are five recognized subspecies of Pacific marten, including *M. c. caurina*, *M. c. humboldtensis* (hereafter, Humboldt marten), *M. c. origenes*, *M. c. sierrae* (hereafter, Sierran marten), and *M. c. vulpina* (Hall 1981). Although both Humboldt and Sierran martens occur in California, Humboldt martens inhabit lower elevation coastal and near-coastal forests that receive little to no snowfall (Slauson et al. 2007, Moriarty et al. 2019), a characteristic unique among Pacific marten subspecies. Sierran martens inhabit forests at relatively high elevations that receive significant winter snowfall (Spencer et al. 1983, Zielinski 2014), typical of forests inhabited by Pacific marten subspecies other than the Humboldt marten (Krohn et al. 1997, Thompson et al. 2012). The Humboldt marten has received considerable conservation attention in recent years, as it was thought to be either extirpated or extremely rare in California in the late 20th century and appears to have a substantially reduced extant distribution relative to historical conditions (Zielinski et al. 2001, Slauson et al. 2019). Subsequently, the Humboldt marten was designated as state endangered in California in 2019 and was listed as threatened under the federal Endangered Species Act as a “distinct population segment” of the Pacific marten in 2020 (California Department of Fish and Wildlife 2019, US Fish and Wildlife Service 2020). Sierran martens have experienced more localized population declines (Zielinski et al. 2005, Moriarty et al. 2011), although potential changes in temperature, snowfall, and fire severity could influence future declines (Spencer et al. 2015, Zielinski et al. 2017).

Despite conservation concern for both subspecies, a limited amount of data are available to assess patterns of Pacific marten reproductive ecology (Green et al. 2017). Given that Humboldt martens inhabit forests that are influenced by dissimilar bioclimatic conditions than forests inhabited by other Pacific martens, it is unclear whether the

reproductive ecology of Pacific martens is consistent among subspecies, and it is further unclear whether the reproductive ecology of the more widely distributed and better-studied American marten is generalizable to Pacific martens. To address these uncertainties, we had two primary research objectives: 1) estimate reproductive parameters for Humboldt and Sierran martens in California, including parturition date, proportion of adult females reproducing, and litter size; and 2) describe den use by Humboldt and Sierran martens. Additionally, we summarized existing information on reproductive parameters and den use from other American and Pacific marten populations across North America to provide a comparison to our study populations. Our findings provide baseline information for assessing Pacific marten population dynamics and characterizing fine-scale Pacific marten reproductive habitat.

Methods

Study Area

Humboldt Marten—The Humboldt marten study area was located in northwestern California (41°20'56"N, 123°47'09"W; Figure 1). Research occurred primarily on private lands owned by Green Diamond Resource Company and the Yurok Tribe, adjacent to lands administered by the US Department of Agriculture (USDA) Forest Service, Six Rivers National Forest. The study area was 120 km² in size, and elevations ranged from 150 to 900 m. Climate was characterized by moderate year-round temperatures, distinct wet and dry periods, and high precipitation amounts in the winter (Jimerson et al. 1996). Annual monthly mean temperatures ranged from 7 to 15 °C, and annual mean precipitation ranged from 75 to 300 cm (California Department of Water Resources 2018). Precipitation fell largely as rain and mean snow depth in April was 0 cm (California Department of Water Resources 2018).

The Humboldt marten study area was characterized by a mix of coniferous and hardwood forest with a spatially extensive shrub understory. Dominant forest types included Douglas-fir (*Pseudotsuga menziesii*) and tanoak (*Notholithocarpus densiflora*) in the eastern portion of the study area,

with redwood (*Sequoia sempervirens*) becoming more common on the western edge. Common conifer species included western hemlock (*Tsuga heterophylla*), Port Orford cedar (*Chamaecyparis lawsoniana*), and western redcedar (*Thuja plicata*). Hardwood species were common and included giant chinquapin (*Chrysolepis chrysophylla*), red alder (*Alnus rubra*), bigleaf maple (*Acer macrophyllum*), and Pacific madrone (*Arbutus menziesii*). Dominant shrub species included salal (*Gautheria shallon*), Pacific rhododendron (*Rhododendron macrophyllum*), evergreen huckleberry (*Vaccinium ovatum*), and red huckleberry (*V. parvifolium*). The majority of private lands within the study area have been intensively managed for timber production, with timber harvest beginning in the 1950s (Yurok Tribal Forestry Department 2012).

Sierran Marten—The Sierran marten study area was located in northeastern California (40°05'51"N, 121°23'53"W; Figure 1) on public lands administered by the USDA Forest Service, Lassen National Forest, 250 km southeast of the Humboldt marten study area. The study area was 100 km² in size and elevations ranged from 1800 to 2100 m. Climate was characterized by hot, dry summers and cold winters with substantial snowfall amounts at higher elevations. Annual monthly mean temperatures ranged from 5 to 16 °C, and annual mean precipitation ranged from 50 to 200 cm (California Department of Water Resources 2018). Mean snow depth in April was 114 cm (California Department of Water Resources 2018).

The Sierran marten study area was characterized by coniferous forest with dominant forest types including red and white fir (*Abies magnifica*, *A. concolor*). Pines (*Pinus* spp.) were less common but included Jeffrey pine (*P. jeffreyi*), lodgepole pine (*P. contorta*), ponderosa pine (*P. ponderosa*), sugar pine (*P. lambertiana*), and western white pine (*P. monticola*). Hardwood species were uncommon and were restricted to riparian areas but included aspen (*Populus tremuloides*), black cottonwood (*P. trichocarpa*), and white alder (*A. rhombifolia*). Natural openings included perennial meadows and areas of bush chinquapin (*Chrysolepis sempervirens*), deer brush (*Ceanothus integerrimus*), mountain whitethorn (*C. cordulatus*), tobacco

brush (*C. velutinus*), and white and green leaf manzanita (*Arctostaphylos manzanita*, *A. patula*). Forests within the study area have been managed at low intensity, primarily for fuels reduction (e.g., Moriarty et al. 2016).

Capture and Monitoring

We studied reproductive female martens as part of two larger research efforts that investigated juvenile marten dispersal patterns (Humboldt marten study area; K. Slauson, unpublished data on file at USDA Forest Service, Pacific Southwest Research Station, Redwood Sciences Lab, Arcata, CA) and patterns of marten rest structure use (Sierran marten study area; Tweedy et al. 2019). We trapped Humboldt martens from September to March of 2013 to 2016 and Sierran martens from September to March of 2015 to 2017. We captured martens using live traps (model 106, Tomahawk Live Traps, Tomahawk, WI), and anesthetized animals using a combination of ketamine (18 or 25 mg kg⁻¹) and midazolam (0.2 mg kg⁻¹; Mortensen and Moriarty 2015). We estimated age at capture and classified each individual as young-of-the-year (≤ 1 year old), yearling (> 1 year old but < 2 years old), or adult (≥ 2 years old; Jonkel and Weckwerth 1963). We removed a vestigial upper premolar tooth for age confirmation via cementum annuli analysis (Poole et al. 1994; Matson's Laboratory LLC, Manhattan, MT), and fit yearlings and adults with a Very High Frequency (VHF) radio-collar (M-1800, Advanced Telemetry Systems, Isanti, MI; MI-2, Holohil Systems LTD., Carp, Ontario, Canada). Capture and immobilization techniques followed guidelines for research with wild mammals (Sikes et al. 2016). Capture procedures were approved by the USDA Forest Service Institutional Animal Care and Use Committee (permit #2015-002; Sierran site only) and permitted by the California Department of Fish and Wildlife (permits #4683, #010793).

Female martens may give birth as early as March, and marten kits typically initiate dispersal between 4 and 6 months of age (Mead 1994, Johnson 2008). Hereafter, we refer to the interval between parturition and kit dispersal as the “denning period”. We monitored radio-collared adult

(≥ 2 years old) martens during the denning period of each year (Humboldt: 2014 to 2016; Sierran: 2016 to 2017) using a combination of VHF radio telemetry and remotely triggered cameras. Initially, we used VHF telemetry to assess whether each female was exhibiting behavior consistent with parturition (e.g., localization of movement for > 1 day or extended periods of inactivity). If localization was indicated, we performed a “walk-in” to identify the natal den (the den where parturition occurs; Ruggiero et al. 1998) and installed ≥ 2 remote cameras (Aggressor Trophy, Bushnell, Overland Park, KS; Hyperfire, Reconyx Inc., Holmen, WI) to monitor activity. We verified reproduction when a female moved a kit or kits from the natal den to a maternal den (any den used subsequent to the natal den but prior to kit dispersal; Ruggiero et al. 1998) and installed cameras at all maternal dens identified. We limited the frequency of visits to dens by only performing walk-ins if we suspected that a female had moved to a new den. We positioned cameras at a distance of 3 to 5 m from each den and checked cameras on ~ 2 week intervals; cameras were left in place for the duration of the denning period.

Based on a combination of VHF telemetry and photographic evidence, we assessed parturition date, proportion of adult females reproducing, and litter size of Humboldt and Sierran martens. We pooled data across years for both subspecies due to small sample sizes. We estimated parturition date based on localization of female activity to a natal den and assumed that parturition occurred < 24 hours after localization (e.g., Kleef and Tydeman 2009). We estimated proportion of females reproducing as the number of adult females that produced a litter of kits divided by the total number of adult females monitored. We calculated the proportion of females reproducing for both combined adult (all females ≥ 2 years old) and age-specific (2 or ≥ 3 years old) classes, as age-specific heterogeneity in this metric has been reported (Thompson and Colgan 1987, Flynn and Schumacher 2009). We estimated litter size based on the number of kits moved by the female upon leaving the natal den. We used 2-tailed *t*-tests to compare parturition dates and litter sizes of Humboldt and Sierran martens and conducted

statistical analyses in R version 3.6.1 (R Core Development Team 2019).

At each natal and maternal den, we determined the den structure type, den location, structure size, and species; we recorded structure data when females were absent to minimize disturbance. We categorized den structure types as live trees, snags, logs, stumps, rock piles, subterranean, or “other”. We categorized den location by position within each structure, as aerial (above ground) or terrestrial (at or below ground). We measured den structure size as diameter at breast height (live trees, snags) or maximum diameter (logs, stumps) and summarized mean diameter for each structure type. We categorized woody den structures as conifer or hardwood and identified them to species. Some den structures were used on a single occasion (“single-use” dens), while other structures were used on repeat occasions (e.g., as a natal den in multiple denning periods; “repeat-use” dens). For total number of dens, we included both single-use and repeat-use dens. For all other den information, we included only single-use dens.

Results

Reproductive Parameters

Humboldt Marten—We radio-tracked nine female Humboldt martens over 15 total denning periods in 2014 to 2016 (Table 1). Mean parturition date was 13 April ± 7.2 days ($\bar{x} \pm SD$; $n = 6$) with a range of 31 March to 21 April (Table 2, Figure 2). Proportion of adult females reproducing was 80% ($n = 12$ of 15) with age at parturition ranging from 2 to 5; 100% ($n = 10$ of 10) of ≥ 3 -year-old females and 40% ($n = 2$ of 5) of 2-year-old females produced a litter of kits. Mean litter size was 1.8 ± 0.6 kits ($n = 11$) with a range of 1 to 3. Two females produced kits, but mothers died prior to kit dispersal; one female was killed by a bobcat on 30 April 2014, and a second female died on 21 June 2016, apparently due to collar entrapment.

Sierran Marten—We radio-tracked six female Sierran martens over eight total denning periods in 2016 to 2017 (Table 1). Mean parturition date was 29 April ± 8.8 days ($n = 7$) with a range of 21

TABLE 1. Summary of reproductive data for adult female Humboldt (*Martes caurina humboldtensis*) and Sierran (*M. c. sierrae*) martens in California, 2014 to 2017. Data include unique female marten identification, year monitored, age of female at time of parturition, parturition date, litter size, and number of dens used. An asterisk (*) indicates adult females that were monitored but did not reproduce in a given year.

Subspecies	Marten ID	Year	Age	Parturition Date	Litter Size	Dens Used
<i>M. c. humboldtensis</i>	F01	2014	5	-	1	1
	F03*	2014	2	-	-	-
	F04	2014	3	-	2	3
	F05	2014	2	-	2	4
	F06	2014	2	-	2	4
	F08	2014	3	-	1	3
	F04	2015	4	10 April	2	3
	F05	2015	3	17 April	2	6
	F06	2015	3	-	-	1
	F08	2015	4	20 April	2	4
	F09*	2015	2	-	-	-
	F04	2016	5	31 March	3	5
	F06	2016	4	15 April	2	6
	F13*	2016	2	-	-	-
	F15	2016	3	21 April	2	2
<i>M. c. sierrae</i>	F15	2016	3	26 April	2	7
	F17	2016	3	24 April	2	10
	F15	2017	4	28 April	2	5
	F17	2017	4	21 April	3	11
	F19	2017	2	10 May	2	5
	F20	2017	3	22 April	1	11
	F21*	2017	2	-	-	-
	F22	2017	2	13 May	1	10

April to 13 May (Figure 2). Proportion of adult females reproducing was 87% ($n = 7$ of 8) with age at parturition ranging from 2 to 4 years old; 100% ($n = 5$ of 5) of ≥ 3 -year-old females and 67% ($n = 2$ of 3) of 2-year-old females produced a litter of kits. Mean litter size was 1.9 ± 0.7 kits with a range of 1 to 3. Compared to Humboldt martens, Sierran marten parturition dates were significantly later ($t_5 = -5.66$, $P < 0.01$) but litter sizes did not differ significantly ($t_{10} = 0.17$, $P = 0.87$).

Den Use

Humboldt Marten— We identified 42 Humboldt marten dens from 2014 to 2016, including 32 (76%) single-use and 10 (24%) repeat-use dens (Table 3). Dens included 11 natal and 31 maternal dens (7 ± 4.5 per female, range 1 to 11) and females used 3.5 ± 1.7 dens in a given denning period (range 1 to 6). Single-use den structure types included 23 live trees (72%; $n = 17$ hardwoods [80.3 ± 18.5 cm

diameter] and $n = 6$ conifers [135.4 ± 57.9 cm]), 5 snags (16%; $n = 4$ conifers [150.8 ± 58.8 cm] and $n = 1$ hardwood [91 cm]), 1 rock pile (3%), 1 log (3%), 1 subterranean (3%), and 1 human-made marten box (3%; see Delheimer et al. 2018). Den location types included 22 aerial cavities (69%), 3 terrestrial (9%), and 7 unknown aerial locations (22%); natal dens were predominantly in aerial cavities in live trees or snags (82%; $n = 9$ of 11). Den structure species included both hardwoods and conifers and consisted of giant chinquapin ($n = 16$), redwood ($n = 5$), Douglas-fir ($n = 4$), tanoak ($n = 2$), western hemlock ($n = 1$), and western redcedar ($n = 1$).

Sierran Marten— We identified 59 Sierran marten dens from 2014 to 2016, including 54 (92%) single-use and 5 (8%) repeat-use dens (Table 3). Dens included 7 natal and 52 maternal dens (11.8 ± 5.8 per individual, range 5 to 21) and females used 8.4 ± 2.7 dens in a given denning period (range 5

TABLE 2. Reproductive parameters of North American martens, based on a review of peer-reviewed publications, unpublished reports, and theses or dissertations. Studies included captive, trapped, and untrapped populations of American martens (*Martes americana*; $n = 19$), Pacific martens (*M. caurina*; $n = 5$), and two populations within the zone of sympatry that could not be identified to species. "ID" for each study corresponds with geographic location in Figure 1. Includes study location (state or province), mean parturition date (n = total number of litters), proportion of females reproducing (n = total number of females), mean litter size (n = total number of litters or corpora lutea count), and source.

Species	ID	Study Type	Location	Parturition Date (n)	Proportion Reproducing (n)		Litter Size (n)	Source
					2 year-old	≥ 3 year-old		
<i>Martes americana</i>	A	Untrapped	Maine	-	-	-	2.0 (2)	Wynne and Sherburne 1984
	B	Untrapped	Maine	-	-	0.81 (48)	-	Payer and Harrison 1999
	C	Untrapped	Michigan	-	-	0.67 (6)	1.8 (4)	Hughart et al. 2013
	D	Untrapped	Michigan	-	-	-	2.7 (13)	Nichols 2016
	E	Untrapped	Minnesota	-	0.56 (16)	0.79 (29)	3.0 (27)	Erb et al. 2014
	F	Untrapped	Ontario	-	-	-	2.2 (9)	Fryxell et al. 2004
	G	Captive	Alberta	05 April (99)	-	-	2.9 (99)	Ritchie 1953
	H	Captive	New York	11 April (2)	-	-	3.0 (2)	Ashbrook and Hansen 1927
	I	Captive	New York	17 April (20)	-	-	2.6 (20)	Markley and Bassett 1942
	J	Captive	Quebec	07 April (5)	-	-	2.2 (5)	Brassard and Bernard 1939
	K	Trapped	Alaska	-	0.13 (141)	0.30 (308)	3.2 (77)	Flynn and Schumacher 2009
	L	Trapped	New Brunswick	-	0.53 (92)	0.64 (139)	2.5 (347)	Pelletier 2005
	M	Trapped	Northwest Terr.	-	0.76 (273)	0.95 (286)	4.0 (476)	Poole and Graf 1996
	N	Trapped	Ontario	-	0.78 (376)	0.93 (504)	3.5 (765)	Strickland and Douglas 1987
	O	Trapped	Ontario	-	0.03 (78)	0.59 (300)	3.2 (180)	Thompson and Colgan 1987
	P	Trapped	Ontario	-	-	0.40 (43)	3.0 (17)	Cobb 2000
	Q	Trapped	Quebec	-	0.60 (83)	0.93 (100)	4.1 (111)	Fortin and Cantin 2004
	R	Trapped	Yukon Terr.	-	0.69 (97)	0.79 (28)	3.5 (89)	Archibald and Jessup 1984
S	Trapped	Yukon Terr.	-	0.52 (81)	0.84 (90)	3.6 (118)	Shults 2001	
<i>Martes caurina</i>	T	Untrapped	California	-	0.20 (15)	1.00 (28)	-	Slauson 2017
	U	Untrapped	California	29 April (7)	0.67 (3)	1.00 (5)	1.9 (7)	This study (<i>M. c. sierrae</i>)
	V	Untrapped	California	13 April (6)	0.40 (5)	1.00 (10)	1.8 (11)	This study (<i>M. c. humboldtensis</i>)
	W	Untrapped	Oregon	-	-	-	1.5 (4)	Bull and Heater 2001
	X	Untrapped	Wyoming	17 April (14)	-	-	1.6 (11)	Henry and Ruggiero 1993
Sympatric	Y	Captive	British Columbia	-	-	-	3.4 (14)	Yerbury 1947
	Z	Trapped	Montana	-	0.85 (110)	0.92 (130)	2.6 (195)	Aune and Schladweiler 1997

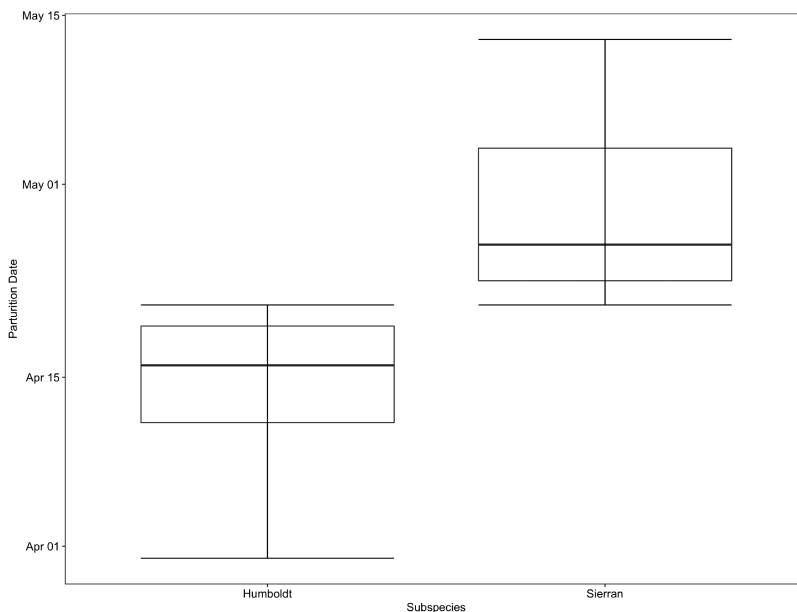


Figure 2. Humboldt (*Martes caurina humboldtensis*) and Sierran marten (*M. c. sierrae*) parturition dates in California, 2014 to 2017. Boxplots display median date (solid line) and 50% quartiles; whiskers represent earliest and latest dates.

to 11). Single-use den structure types included 25 snags (46%; 107.6 ± 30.5 cm diameter), 12 live trees (22%; 105.2 ± 33.2 cm), 9 stumps (17%; 114.1 ± 31.3 cm), 6 logs (11%; 75.2 ± 23.7 cm), and 2 rock piles (4%). Den location types included 35 aerial cavities (65%), 16 terrestrial (30%), and 3 unknown aerial locations (5%); natal dens were exclusively in aerial cavities in live trees or snags (100%; $n = 7$ of 7). Den structure species included conifers only and consisted of white fir ($n = 27$) and red fir ($n = 25$).

Discussion

Reproductive Parameters

Our research indicates that Humboldt and Sierran marten reproductive parameters were largely consistent, although parturition date was the notable exception. Sierran marten parturition dates were approximately three weeks later on average than Humboldt marten parturition dates and were the latest reported date for a North American marten population, while Humboldt marten parturition dates were similar to other North American martens (Table 2). We acknowledge that few studies

of either American or Pacific martens are available for comparison and that our estimates of parturition dates for both Humboldt and Sierran martens are similarly based on limited data. Nonetheless, our estimates indicate little overlap in timing of Humboldt and Sierran marten parturition, despite our study populations occurring at similar latitudes and in close geographic proximity. Given that the onset of active pregnancy in many mustelid species appears to be correlated

with increased photoperiod (Mead 1994)—i.e., populations that occur at similar latitudes should give birth at similar times—the discrepancy between Humboldt and Sierran marten parturition dates suggests that timing of marten parturition may be affected by additional factors. For example, the range of the Sierran marten is characterized by deep spring snowpacks, a bioclimatic feature not present in the range of the Humboldt marten; later Sierran marten parturition dates could be influenced by availability of prey resources important to supporting reproduction (e.g., ground-dwelling sciurids; Slauson and Zielinski 2017, Slauson and Zielinski 2019), whose emergence from hibernation is strongly correlated with spring snowmelt (e.g., Bronson 1980).

While martens are capable of producing their first litter at two years old, some martens may not give birth to their first litter until three years old, and not all adult females may reproduce in a given year (Strickland and Douglas 1987). Accordingly, studies of American martens have universally indicated that 2-year-olds reproduce in a lower proportion than ≥ 3 -year-olds, with 2-year-old American martens reproducing at a

TABLE 3. Den use by North American martens based on a review of peer-reviewed publications, theses or dissertations. Studies consisted of untrapped populations of American martens (*Martes americana*; $n = 3$), and Pacific martens (*M. caurina*; $n = 5$) and only included those that reported structure type and structure size metrics. Den structure types in most studies of American and Pacific martens were dominated by live trees, snags, and logs; “other” structure types include rock piles, slash piles, squirrel middens or nests, and subterranean locations. Structure size indicates mean diameter-at-breast-height (live trees, snags) or mean maximum diameter (logs). We combined live tree and snag structure sizes here to provide a comparison to previous studies, although we report hardwoods (first/smaller value) and conifers (second/larger value) separately for Humboldt martens. A dash (-) indicates an unreported value.

Species	Location	Dens (<i>n</i>)	Structure Type (%)				Structure Size (cm)		Structure Species		Source
			Live Tree	Snag	Log	Other	Live Tree/ Snag	Log	Hard- wood	Conifer	
<i>Martes americana</i>	Wisconsin	7	71%	14%	14%	0%	56	-	-	-	Gilbert et al. 1997
	Michigan	19	84%	11%	5%	0%	52	-	-	-	Hughart et al. 2013
	Michigan	60	85%	12%	3%	0%	54	-	98%	2%	Nichols 2016
<i>Martes caurina</i>	Oregon/ Washington	57	35%	23%	19%	23%	92	-	0%	100%	Raphael and Jones 1997
	Wyoming	115	2%	25%	16%	58%	56	53	0%	100%	Ruggiero et al. 1998
	Oregon	30	27%	13%	27%	24%	83	73	0%	100%	Bull and Heater 2000
	California	32	72%	16%	3%	9%	81/142	-	65%	35%	This study (<i>M. c. humboldtensis</i>)
California	54	22%	46%	11%	21%	107	75	0%	100%	This study (<i>M. c. sierrae</i>)	

roughly 25% lower rate on average (Table 2). The proportion of martens reproducing can vary widely between populations (Table 2), can vary within populations between years, and are predicted to be particularly low in years of reduced prey availability (Thompson and Colgan 1987, Flynn and Schumacher 2009). Nonetheless, our results and the results of another study in California (Slauson 2017) corroborate the finding for Pacific martens that 2-year-olds reproduce in a lower proportion than ≥ 3 -year-olds; 100% ($n = 43$ of 43) of ≥ 3 -year-old martens in our three study populations reproduced, compared to only 30% ($n = 7$ of 23) of 2-year-old martens (Table 2).

Our litter size estimates fell within a similar range to previous reports for Pacific martens (Henry and Ruggiero 1993, Bull and Heater 2001) and together suggest that Pacific martens average slightly less than two kits per litter (Table 2). A brief review further indicates that Pacific marten

litter sizes are significantly smaller than American marten litter sizes across studies ($t_{18} = 7.09$, $P < 0.001$; Table 2) and that American martens average almost three kits per litter. However, litter size estimates are relatively common for American martens, while information on Pacific martens is limited to few studies (Table 2). As such, it remains unclear whether the apparent discrepancy in litter size between American and Pacific martens reveals a consistent pattern, although methodology could offer some explanation for differences between studies. Inspections of reproductive tracts (e.g., counts of blastocysts, corpora lutea, or placental scars) are often used to estimate litter size in populations of trapped carnivores (e.g., Gilbert 1987, Chilelli et al. 1996, Mowat et al. 1996), and accordingly, American marten litter size estimates have predominantly been derived from counts of corpora lutea from carcasses of trapped martens (Table 2). Such counts could result in overestimates; for example, litter sizes larger

than three have commonly been documented *in utero* from carcasses of trapped wolverines (*Gulo gulo*) but have never been observed for live wolverines (Mowat et al. 2020). Observations from untrapped populations could conversely result in underestimates; for example, marten kits in our study could have died prior to detection at the natal den, although studies of the closely related fisher (*Pekania pennanti*) have indicated that kit abandonment at the natal den is an infrequent occurrence (Matthews et al. 2013, Green et al. 2018, Matthews et al. 2019).

Den Use

Prior to our research, only a handful of marten dens have been described in California (Grinnell et al. 1937, Simon 1980, Slauson and Zielinski 2009). In our study, both Humboldt and Sierran martens predominantly used woody structures as dens; in particular, live trees, snags, and logs accounted for 91% and 79% of all dens identified, respectively. This pattern appears to be generally consistent among studies of both Pacific and American martens, with most studies reporting > 75% of dens in live trees, snags, and logs (Table 3). Similar to other Pacific marten subspecies, woody structures used by Sierran martens as dens were comprised exclusively of conifer species (Table 3). Unlike other Pacific marten subspecies and more similar to American martens, woody structures used by Humboldt martens as dens were comprised of both hardwoods (65%) and conifers (35%; Table 3). This result is indicative of the unique composition of forests inhabited by Humboldt martens compared to other Pacific marten subspecies. Whereas most Pacific marten populations occur in higher elevation conifer-dominated forests where hardwoods are largely uncommon, Humboldt martens occur in relatively low-elevation forests that may contain a diversity of hardwood species.

Humboldt and Sierran martens appear to use woody structures as dens that were larger in average diameter than available but unused structures, similar to that reported for Pacific martens in Wyoming (Raphael and Jones 1997) and American martens in Michigan (Nichols 2016), although

we did not perform formal selection analyses to investigate probability of den structure use compared to structure availability (e.g., via a resource selection function; Manly et al. 1993). Nonetheless, Humboldt marten den structures in our research were similar in diameter to Humboldt marten rest structures, which were among the largest size classes available (Slauson and Zielinski 2009). Sierran marten den structures (mean diameter = 104 cm) were also similar in diameter to Sierran marten rest structures (mean diameter = 98 cm; Tweedy et al. 2019), which were almost twice the size of sampled available but unused structures (mean diameter = 53 cm; Tweedy et al. 2019). Given the preponderance of cavity use in our research—airial cavities in live trees and snags represented 66% of all den locations and 89% of natal den locations, when including both study populations—large diameter live trees and snags may be requisite to providing cavities of sufficient size to house a female marten and her kits. As suggested for the cavity-obligate fisher (Matthews et al. 2019), such structures may offer further benefits such as thermal insulation, mediation of environmental conditions, and protection from predators.

Management Implications

Our research indicates that the reproductive ecology of Pacific martens, including our focal populations, is largely consistent among subspecies with the exception of timing of parturition. Anthropogenic disturbances such as timber harvest, outdoor recreation (e.g., Heinemeyer et al. 2019), or research activities that occur during critical reproductive periods such as parturition or lactation can exacerbate energetic stress (Williams et al. 2006, Rode et al. 2007), affect reproductive success (Phillips and Alldredge 2000, French et al. 2011), and influence behavior (Copeland 1996, Paragi et al. 1996) of female mammals, yet avoiding or reducing disturbance requires knowledge of when such periods occur. Site-specific data to account for potential local variability in timing of reproduction may offer the most appropriate guidance for conservation actions and management decisions intended to minimize disturbance to reproductive martens.

The reproductive ecology of Pacific and American martens appears similarly consistent between species, with the exception of litter size. Accurate information on vital rates such as litter size is necessary to evaluate population trends, as variation in vital rates can influence whether a population appears to be increasing, stable, or declining (Cole 1954, Caswell 1978). Marten demographic models and population viability analyses (Buskirk et al. 2012, Manlick et al. 2017, Linnell et al. 2018, Slauson et al. 2019) have commonly incorporated a mean litter size of three kits, based on data from studies of American martens (e.g., Strickland and Douglas 1987). However, out of 33 Pacific marten litters documented, only two litters (6%) had three kits and none had more than three (Table 1, Table 2), suggesting that Pacific marten litter sizes may be smaller than American martens. A litter size of two kits may be a more conservative estimate for Pacific martens, a potential consideration for assessing capacity for growth of Pacific marten populations.

Both Humboldt and Sierran martens predominantly used large diameter woody structures as dens, with live trees and snags appearing particularly important. Identification, retention, and recruitment of similar structures may serve as a foundation for strategies intended to sustain or restore Pacific marten denning habitat. Hardwoods > 70 cm and conifers > 90 cm in diameter encompassed approximately 95% of live trees and snags used as dens by Humboldt and Sierran martens and represent appropriate size classes that could be targeted for retention or recruitment. Specifically, live trees and snags that have existing cavities,

live trees with indications of decay (e.g., heart rot conks), or live trees with pathways for decay that could lead to cavity production (e.g., broken tops, broken branches, and wounds/scars; Bull et al. 1997) would support Pacific marten reproduction by providing both a current and potential future supply of important den locations.

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