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Behavior Patterns of Denning Pacific Martens (*Martes Caurina*)

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***Abstract.*—Reproductive success has substantial implications for mammal populations yet evaluating female behavior during critical reproductive periods can be particularly difficult for cryptic species. North American martens (American Marten, *Martes americana*; Pacific Marten, *M. caurina*) are small-bodied, solitary, and wide-ranging carnivores of conservation concern, whose reproductive behaviors have largely been observed in captive populations. Our primary objective was to assess duration of den use and den attendance patterns of wild female Pacific Martens relative to stages of marten kit development. We tracked five individual female Pacific Martens over seven denning periods in 2016–2017 in the Lassen National Forest, California, using a combination of radio-telemetry and remotely triggered cameras. Pacific Martens used natal dens for significantly longer periods of time than maternal dens (19.6 ± 15.2 [standard deviation] d vs. 5.5 ± 7.5 d; t = -6.168, $P < 0.001$) and spent significantly less time away from the den during lactation than after the onset of weaning (2.8 ± 1.7 h/d vs. 5.5 ± 3.0 h/d; t = -3.544, $P = 0.002$). Following first detection (i.e., removal from the natal den), kits were semi-mobile at 60.6 ± 5.3 d, were mobile at 86.9 ± 4.4 d, and were independent at 153.6 ± 26.3 d, although we estimated that four kits (31%) died prior to independence. Female Pacific Marten behavior was consistent with a central-place foraging strategy and appears to be closely tied to kit developmental stage. Our results indicate that the 2–3 mo following parturition are a critical and sensitive period for both female Pacific Martens and their kits.**

Key Words.—behavior; California; den; foraging strategy; Pacific Marten; remote camera; reproduction; telemetry.

Introduction

Rearing offspring from parturition to independence is a critical portion of the reproductive cycle for female mammals and reproductive success has substantial implications for population dynamics (Heppell et al. 2000). Observing and describing behavior of wild animals during reproduction can be inherently difficult, however, especially for secretive or cryptic species. For example, North American martens (American Marten, *Martes americana*; Pacific Marten, *M. caurina*) are solitary carnivores that have large home ranges relative to their small body size (Buskirk and MacDonald 1989), may exhibit arrhythmic diel activity patterns (Zielinski et al. 1983; Foresman and Pearson 1999), and commonly rear their kits in concealed locations such as tree cavities (Bull and Heater 2000). Marten behavior during kit-rearing has largely been observed in captive animals, which may not be subject to the same stressors as wild animals, such as the energetic costs of acquiring food or variability in environmental conditions (e.g., temperature or precipitation; Cuthill 1991; McPhee and Carlstead 2010). Discerning patterns of behavior in wild female martens may inform whether or how behavior influences reproductive success.

In general, reproduction incurs substantial energetic requirements for female mammalian carnivores (Harvey 1986; Gittleman and Thompson 1988). For instance, female energetic expenditures by the closely related Fisher (*Pekania pennanti*) while rearing kits may be more than 2–3 times greater than expenditures during non-reproductive periods (Powell and Leonard 1983). While the long, thin body profile of a marten confers advantages when hunting prey such as small mammals (Andruskiw et al. 2008), there are also energetic consequences, including a high metabolic rate and a limited ability to store substantial body fat reserves (Buskirk and Harlow 1989). In non-reproductive periods, female martens must consume >700 kJ/d or roughly 1/5 of their body mass in prey to balance energetic expenditures (Gilbert et al. 2009; Martin et al. 2020), equivalent to two chipmunks (*Tamias* spp.) or eight Deer Mice (*Peromyscus maniculatus*; Martin et al. 2020). During kit-rearing, female martens must meet their own energetic requirements as well as those of their growing offspring, which likely obligates them to increase food acquisition, decrease energetic expenditures, or both.

Some have postulated that a central-place foraging strategy is exhibited by female martens during critical reproductive periods such as lactation (Slauson and Zielinski 2019). In theory, central-place foraging should allow female martens to optimize their energetic budgets by maximizing foraging effort while minimizing energy expended (e.g., Orians and Pearson 1979). A variety of behaviors could be indicative of such a strategy, including reproductive female martens selectively capturing prey whose body size most closely approximates their daily energetic needs (Slauson and Zielinski 2019), positioning dens proximal to abundant prey resources (Pearson and Ruggiero 2001), or synchronizing activity periods

with activity of their primary prey (Nichols 2016). Alterations to behavior patterns during reproduction that incur increased energetic expenditures may have fitness consequences (French et al. 2011; Leblond et al. 2013). For martens, traveling increased distances to forage, relocating kits to new dens, or modifying activity periods could influence fitness outcomes such as female survival.

Despite the potential ramifications for marten fitness, information is lacking on many behavioral aspects of wild martens during denning periods. Therefore, our primary objective was to describe fine-scale patterns of denning behavior by female Pacific Martens, including duration of den use, den attendance, stages of kit development, and kit survival. Characterizing behavior patterns may reveal critical portions of the denning period when female martens and their kits are most vulnerable, the identification of which can direct future research and guide management actions intended to support successful marten reproduction.

Methods

Study area.—Our study area was in the Lassen National Forest in northeastern California, encompassing an area of approximately 100 km^2, at elevations ranging from 1,800–2,100 m (Fig. 1). Annual mean temperatures ranged from 5–16° C, annual mean precipitation ranged from 50–200 cm, and mean snow depth in April was 114 cm (http://cdec.water.ca.gov/snow/). The study area was montane and largely forested but intermixed with shrub fields, perennial meadows, and riparian corridors. Forests were conifer-dominated, primarily Red Fir (*Abies magnifica*) and White Fir (*A. concolor*), but also including Incense Cedar (*Calocedrus decurrens*), Jeffrey Pine (*Pinus jeffreyi*), Lodgepole Pine (*P. contorta*), Ponderosa Pine (*P. ponderosa*), Sugar Pine (*P. lambertiana*), and Western White Pine (*P. monticola*). Common shrub species included Bush Chinquapin (*Chrysolepis sempervirens*), manzanita (*Arctostaphylos* spp.), and Tobacco Brush (*Ceanothus velutinus*). Hardwood trees (e.g., Aspen, *Populus tremuloides*) were uncommon and restricted to riparian and stream corridors.

Data collection.—We captured Pacific Martens from September 2015 to March 2017 using live traps (model 106, Tomahawk Live Traps, Tomahawk, Wisconsin) and anesthetized martens using a combination of ketamine and midazolam (Mortensen and Moriarty 2015). We determined sex and age, weighed Pacific Martens, and removed a vestigial upper premolar tooth to confirm age via cementum annuli analysis (Poole et al. 1994; Matson's Laboratory LLC, Manhattan, Montana). We classified individuals as young-of-the-year (< 1 y old), yearling (1–2 y old), or adult (≥ 2 y old; Jonkel and Weckwerth 1963) and fitted yearlings and adults with a VHF radio-collar (28 g; M-1800, Advanced Telemetry Systems, Isanti, Michigan). Capture techniques adhered to guidelines for research with wild mammals established by the American Society of Mammalogists (Sikes et al. 2016).

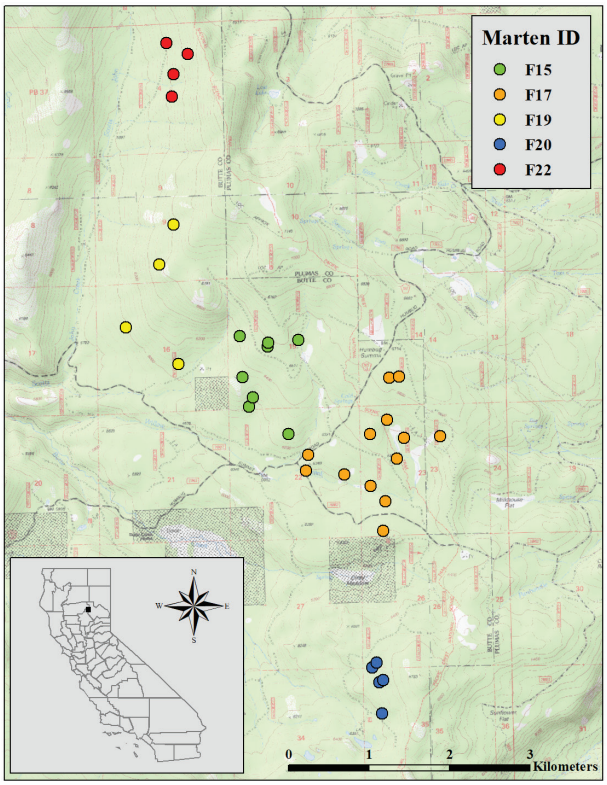

Figure 1. Study area in the Lassen National Forest, California. Points indicate the 34 dens monitored for use by female Pacific Martens (*Martes caurina*) and their kits in 2016–2017.

We tracked radio-collared female Pacific Martens during denning periods (i.e., expected parturition to beginning of kit dispersal; Johnson et al. 2009; Delheimer et al. 2021) from approximately mid-April to late-September. We assessed behavior consistent with parturition (e.g., localization of movement or inactivity for > 24 h; Kleef and Tydeman 2009) and when indicated, we used homing techniques to identify the natal den (e.g., the location of parturition; Ruggiero et al. 1998) and assumed that parturition occurred within 24 h (Kleef and Tydeman 2009). We considered any location used after the natal den but prior to kit dispersal to be a maternal den (Ruggiero et al. 1998; Robitaille et al. 2020) and confirmed each as a den by presence of kits. At all dens identified, we installed two or more remotely triggered cameras (Aggressor Trophy, Bushnell, Overland Park, Kansas or Hyperfire, Reconyx Inc., Holmen, Wisconsin). We checked cameras on an approximately two week interval, when the female marten was absent to reduce disturbance, and we left cameras in place for the duration of the denning period, similar to other den monitoring methods (Green et al. 2017; Smith et al. 2020).

We processed photographs from den monitoring using Picasa software (version 3.9.141; Google LLC, Mountain View, California). Data had a non-normal distribution with unequal variances and we log-transformed (den use duration) and square root-transformed (den attendance)

data prior to analysis, which met assumptions of parametric tests. We compared duration of den use (days) by female Pacific Martens between natal and maternal dens, using a Two-tailed *t*-test and a significance level of $P \leq 0.05$. For den attendance, we determined Away Events (Henry et al. 1997) by pairing instances of females leaving their dens with subsequent instances of females returning to their dens. We calculated the sum of the duration (minutes) of away events by a female during each daily or 24-h period (0000–2359) and then binned daily events by each week following parturition (e.g., days 1–7 = week 1, days 8–14 = week 2). We considered weeks 1–6 to be the Lactation Period and weeks 7–8 to be the Early Weaning period, as weaning begins when kits are approximately 42 d old (Brassard and Bernard 1939). We used a Two-tailed *t*-test and a significance level of $P \leq 0.05$ to compare duration of daily away events between lactation and early weaning and calculated average duration of away events by week. We did not estimate den attendance after eight weeks, as females began to move dens frequently, kits became increasingly active, and we were unable to determine if kits remained at the den during away events or were traveling with their mother.

We described stages of Pacific Marten kit development by estimating dates for advancements that likely corresponded with decreasing levels of dependence and increasing levels of coordination (e.g., ability to travel without assistance, hunt or forage, or escape predators). Developmental advancements included: (1) first detection; removal of kits from the natal den by the female; (2) semi-mobility; evidence of kits active outside of the den in the presence of the female; (3) mobility; evidence of kits active outside of the den, in the absence of the female; and (4) independence; evidence that kits were no longer with the female (e.g., detections of the female with no kits present, and no kits subsequently detected). Marten kits may disperse as early as 4 mo of age (Johnson et al. 2009) and we assumed that kits < 4 mo old that we could no longer account for had died and that 4 mo old was the minimum age for kit independence.

We estimated monthly kit survival in the first 4 mo following parturition (May, June, July, and August) and calculated kit survival as the number of kits observed at the end of each month divided by the total number of kits produced. While it is possible that kits were abandoned at the natal den, Fisher studies have indicated this as an infrequent occurrence and unverifiable without climbing the natal den to perform kit counts (Matthews et al. 2013; Green et al. 2018; Matthews et al. 2019). We assumed that no kits died prior to first detection when initially estimating number of kits produced (see Delheimer et al. 2021) and subsequently estimating survival. Similar to our estimates of kit independence, to estimate survival we assumed that kits < 4 mo old that we could no longer account for had died. Given that we did not radio-collar kits and could not assess their ultimate fates, survival estimates represent minimum numbers of presumed kit deaths.

Results

Den use and attendance.—We tracked five female Pacific Martens over seven denning periods in 2016–2017. We assessed use of 34 individual den structures (Figs. 1, 2); some structures were used more than once as

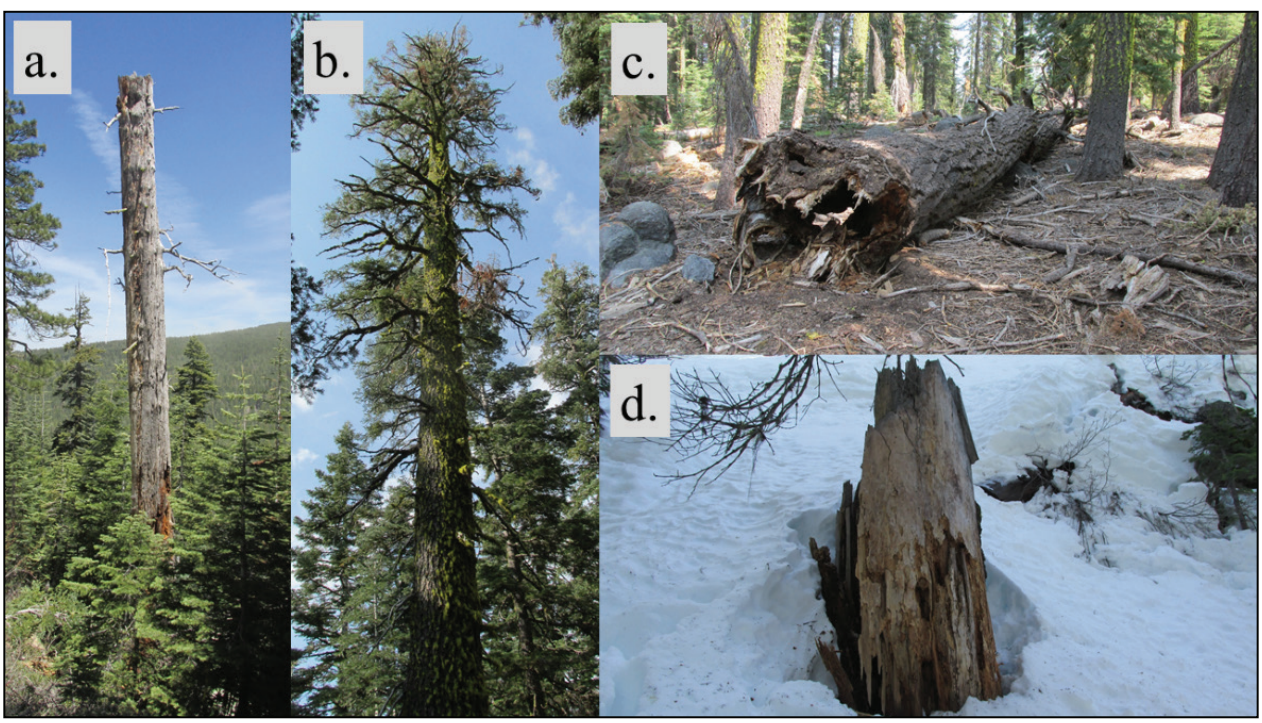

Figure 2. Examples of the most commonly used den types by female Pacific Martens (*Martes caurina*) in the Lassen National Forest, California, in 2016–2017: (a) snags, (b) live trees, (c) logs, and (d) stumps. (Photographed by Matthew Delheimer).

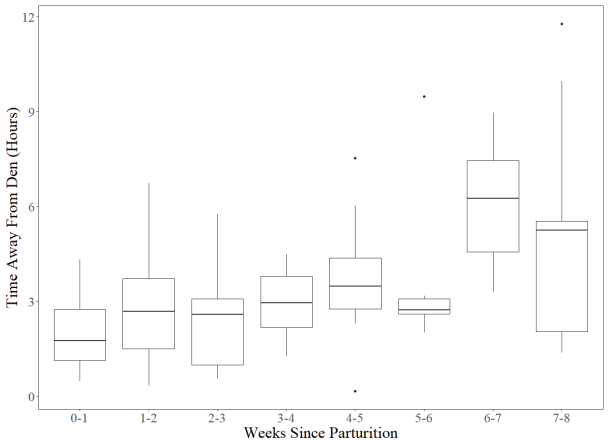

Figure 3. Weekly medians (horizontal lines) of daily time spent away from the den by female Pacific Martens (*Martes caurina*) in the Lassen National Forest, California, in 2016–2017. Boxes bound 25% and 75% quartiles, and black dots represent extreme values.

a den within a denning period and we determined duration of use for a total of seven natal dens and 66 maternal dens, respectively. Pacific Martens used natal dens for significantly longer amounts of time than maternal dens (t = -6.168, df = 12, P < 0.001). Natal dens were used for 19.6 ± 15.2 d (mean ± standard deviation; range, 7–50 d), including live trees (14.9 ± 8.7 d; n = 5) and snags (31.1 ± 26.5 d; n = 2). Maternal dens were used for 5.5 ± 7.5 d (range, 1–35 d), including snags (8.6 ± 9.7 d; n = 28), logs (2.3 ± 3.3 d; n = 13), live trees (4.6 ± 6.1 d; n = 12), stumps (2.3 ± 2.1 d; n = 9), and rock piles (3.6 ± 2.7 d; n = 4).

We documented 110 away events by female Pacific Martens during lactation (n = 75 events; kit age = 0–42 d) and early weaning (n = 35 events; kit age = 43–56 d). Daily time spent away from the den was significantly lower during lactation than early weaning (t = -3.544, df = 19, P = 0.002) with Pacific Martens spending 2.8 ± 1.7 h and 5.5 ± 3.0 h away during lactation and early weaning, respectively. Pacific Martens spent the least time away from the den in the first week after parturition (2.0 ± 1.2 h/day; Fig. 3) and left for as little as 0.5 h per day. Time spent away from the den generally increased from 2.7 ± 1.7 h/day in the second week after parturition to 3.8 ± 2.8 h per day in the sixth week after parturition (Fig. 3). Time spent away from the den increased substantially beginning in the seventh week after parturition (i.e., at the onset of weaning) to 6.1 ± 2.1 h/day.

Stages of kit development and survival.— Pacific Marten kits were typically small and immobile upon first detection at 19.6 ± 15.2 d (median date = 19 May). Kits were moved from the natal den to the first maternal den by being scruffed (moved by the neck) by the female, regardless of age (Fig. 4). Kits were moved one-at-a-time and in litters > 1, kits were moved an average of 19.7 ± 15.2 min apart (range, 6–36 min). Kits were semi-mobile at 60.6 ± 5.3 d (range, 54–68 days; median date = 1 July), mobile at 86.9 ± 4.4 d (range, 82–95 d; median date = 27 July), and appeared to be independent

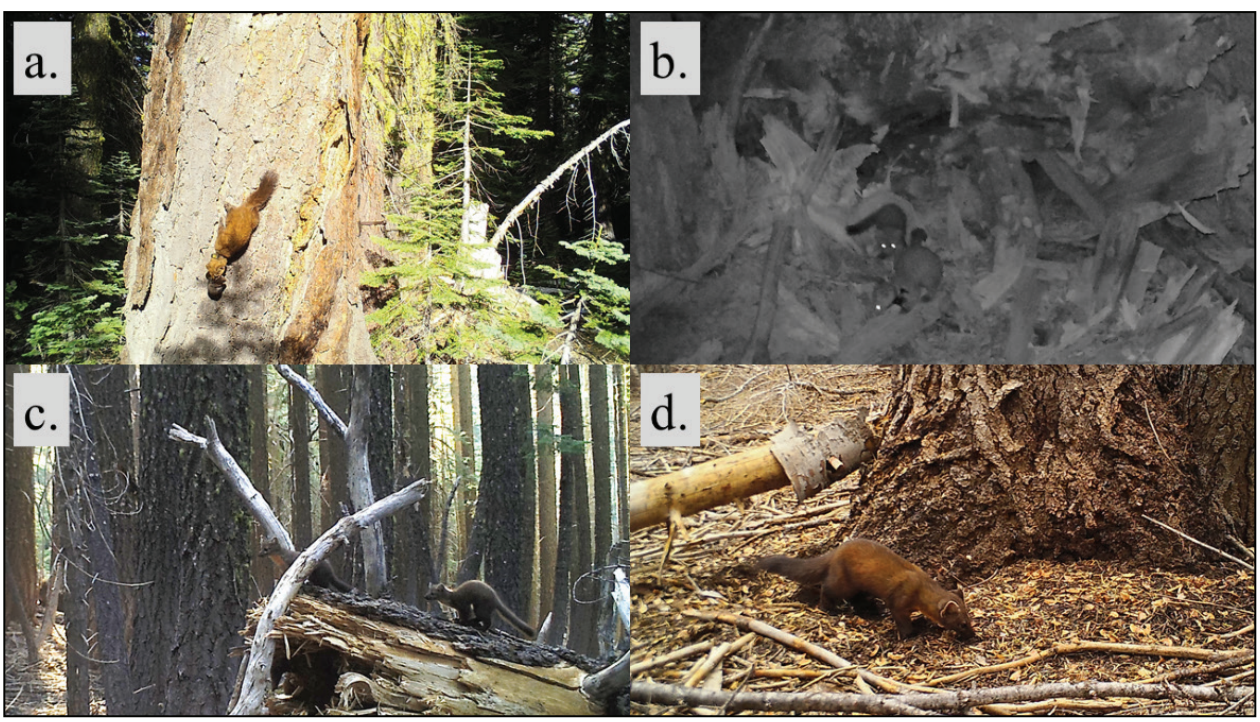

Figure 4. Stages of kit development of Pacific Martens (*Martes caurina*) in the Lassen National Forest, California, in 2016–2017: (a) first detection (about 20 d old), kit is scruffed in mouth of mother; (b) semi-mobility (about 60 d old); (c) mobility (about 90 d old); and (d) independence (about 150 d old). (Photographed using remotely triggered cameras: Aggressor Trophy, Bushnell, Overland Park, Kansas or Hyperfire, Reconyx Inc., Holmen, Wisconsin).

at 153.6 ± 26.3 d (range, 131–195 d; median date = 29 September).

We documented the loss or presumed mortality of zero Pacific Marten kits in the months of April, May, and June, one kit in July, and three kits in August. Based on initial litter size determinations, we estimated that four of 13 kits (31%) died prior to presumed independence. While we were unable to assess most sources of presumed mortality, we suspected that two kits were killed by a Bobcat (*Lynx rufus*) outside of a maternal den in August, based on photographs and forensic evidence.

Discussion

Our results indicate that both duration of den use and daily time spent at the den by female Pacific Martens decreased with increased kit age, corroborating previous evidence that female martens exhibit behavior consistent with a central-place foraging strategy (e.g., Pearson and Ruggiero 2001; Slauson and Zielinski 2019). Female marten behavior during denning appears to be largely driven by the needs of their kits at different developmental stages, although other factors (e.g., changing caloric needs or continued territory maintenance) are likely to influence female behavior as well. Pacific Martens used natal dens on average for significantly longer periods of time than maternal dens (20 d versus 6 d), which was relatively short compared to previous reports of other North American marten populations (43 d; Henry and Ruggiero 1993) and European Pine Martens (*M. martes;* 56 d; Kleef and Tydeman 2009). Den relocation, particularly moving from the natal den to the first maternal den, likely requires a substantial energetic expenditure by female martens (e.g., physically moving kits from one den to another) while also exposing both the female and her kits to predation. It is reasonably intuitive then, that female martens should occupy natal dens for a relatively long duration. The benefits of den relocation, however, likely increase over time as kits increase in size, prey resources near the natal den are depleted, or feces, parasites, or prey remains begin to accumulate in the den (Henry and Ruggiero 1993; Nichols 2016). Although it is often unclear why den relocation occurs, including in our study, a suite of other factors have been suggested as influential to den relocation including presence of predators or male martens at dens, observer disturbance, kit death, or limited availability of other suitable den locations (Henry and Ruggiero 1993; Kleef and Tydeman 2009; Nichols 2016).

Female Pacific Martens spent significantly increased amounts of time away from the den during weaning compared to lactation, and although this finding has previously been reported for martens (Henry et al. 1997; Kleef and Tydeman 2009), our study is the first to present even finer-scale patterns. Similar to female Fishers in California (Cummins 2016), female Pacific Martens spent the least amount of time away from the den in the first week following parturition and spent generally increasing amounts of time away from the den in subsequent weeks during lactation. We acknowledge that our numbers of away events represent minimum estimates, as we were not always able to pair instances of females leaving the den with returning to the den, or vice-versa. Yet given that marten kits are born blind, sparsely-furred, and weighing only 28g (Ashbrook and Hansen 1927) and are completely dependent on their mothers (e.g., for food in the form of milk), our results are consistent with the premise that female martens are obligated to minimize time away from the den in the weeks immediately following parturition. As kits grow larger and require more food resources, females may have to spend more time or travel further distances to acquire sufficient prey, with the trade-off that their growing kits should require less provisioning of other resources (e.g., body heat). Because lactation is a particularly taxing phase of raising offspring (Gittleman and Thompson 1988), the onset of weaning and an increasing ability to deliver solid foods may relax energetic stress on female martens, despite the increasing energetic requirements of their kits.

Pacific Marten kit development following the onset of weaning appears to occur rapidly: for example, captive marten kits did not fully open their eyes until 37–39 d yet ventured forth from the den by 45–56 d (Ashbrook and Hansen 1927; Brassard and Bernard 1939). Indeed, in our study, weaning coincided with a marked decrease in den attendance by females, followed shortly by coordinated movement by kits outside of the den (accompanied by the female) by approximately eight weeks old. By 12 weeks old, kits in our study were active outside of the den while the female was away, corresponding with the time at which marten kits achieve full body length (Brassard and Bernard 1939) and develop the ability to climb trees (Henry and Ruggiero 1993). This important developmental advance was not without consequence, as 75% (3 of 4) of suspected kit mortalities occurred when kits were approximately three months old, two of which we attributed to Bobcat predation. Bobcats appear to be common predators of adult martens (Bull and Heater 2001; Woodford et al. 2013; Wilk and Raphael 2018) and may also be important predators of kits. Although we detected male Pacific Martens, which may kill other adult martens and unweaned kits (Bull and Heater 2001; Dubruiel et al. 2013), as well as several other potential predator species at dens (Coyote, *Canis latrans*; Fisher; Mountain Lion, *Puma concolor*; Fig. 5), there was no indication that species other than Bobcats were responsible for kit mortalities during our study.

The 3 mo following parturition appears to be the most critical portion of the denning period for martens. For the first 2 mo, marten kits are completely dependent on their mothers for food and such a degree of kit dependence may have fitness consequences for females. For example, survival of adult female Pacific Martens

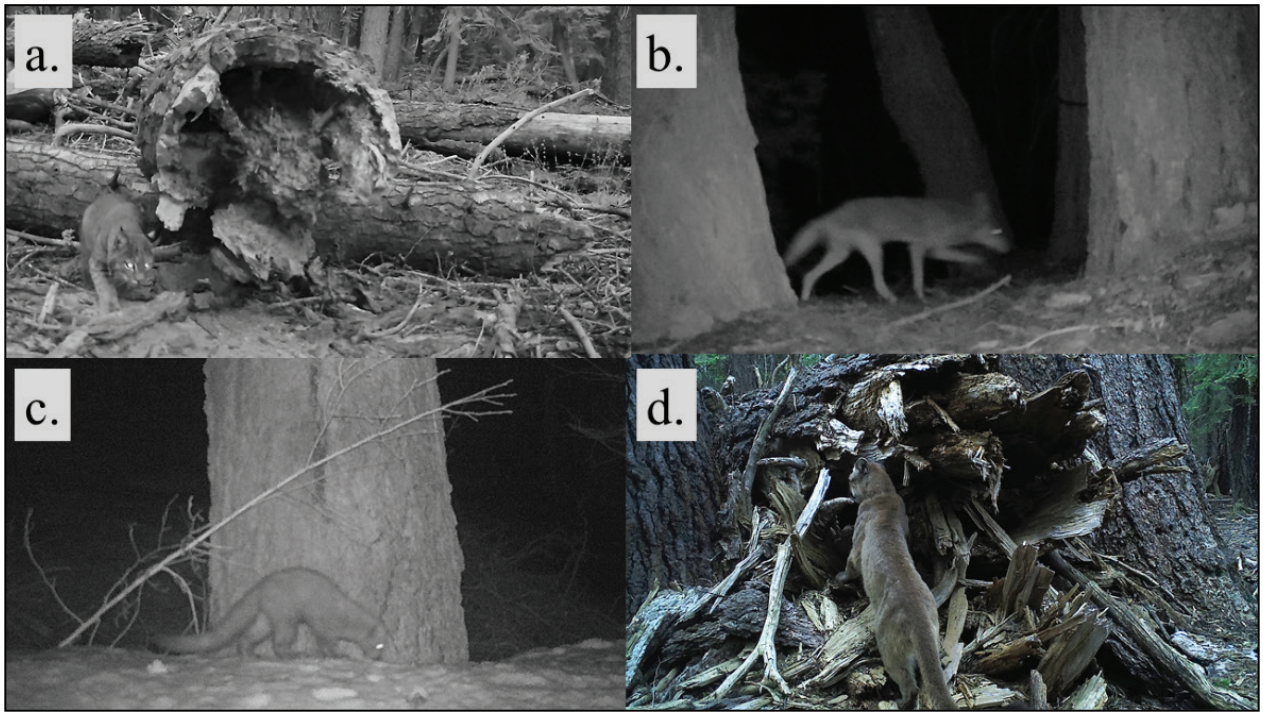

Figure 5. Examples of potential predators detected at Pacific Marten (*Martes caurina*) dens in the Lassen National Forest, California, in 2016–2017: (a) Bobcat (*Lynx rufus*), (b) Coyote (*Canis latrans*), (c) Fisher (*Pekania pennanti*), and (d) Mountain Lion (*Puma concolor*). We suspected that a Bobcat was responsible for the loss of a litter of two kits. (Photographed using remotely triggered cameras: Aggressor Trophy, Bushnell, Overland Park, Kansas or Hyperfire, Reconyx Inc., Holmen, Wisconsin).

was lowest from March to May in Oregon (Wilk and Raphael 2018), which would directly correlate to the timing of active pregnancy through lactation in our study area (Delheimer et al. 2021). In another population in Oregon, 50% of female Pacific Martens died before their kits were independent (Bull and Heater 2001). The death of a female marten at any time prior to kit independence could result in the death of her kits as well; if the female died within the first 2 mo, kit death would be an almost certain outcome, resulting in the simultaneous loss of multiple generations. Given that martens exhibit delayed sexual maturity and produce small numbers of offspring, despite their relatively short lifespans (Strickland and Douglas 1987), such losses could have important implications for marten population dynamics (Buskirk et al. 2012).

The third month following parturition may bring about more direct survival consequences for kits. Although now capable of traveling with their mothers, kits of this age have not reached adult body size, are likely still gaining coordination and agility, and may be most susceptible to predation. For instance, two of three Pacific Marten litters that did not survive to independence in Wyoming were lost in the third month (65 and 76 d post-parturition, respectively; Henry and Ruggiero 1993). We similarly documented the loss of a kit during the third month and an additional three kits in the following month, prior to presumed independence. Kit survival may not improve subsequent to independence: for instance, only 38% of kits (54 of 143) survived from dispersal initiation to adulthood in Canada (Johnson et al. 2009). Given this, developing management strategies that support female martens and their kits during their most vulnerable times may represent the best opportunity to influence marten reproductive success. Further investigations that better elucidate relationships between behavior patterns and survival outcomes may offer vital information to guide such strategies.

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