

Reproductive Ecology of the Fisher (*Pekania pennanti*) in the Southern Sierra Nevada:
An Assessment of Reproductive Parameters and Forest Habitat Used by Denning Females

By

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ABSTRACT

Quantifying reproductive parameters and characterizing habitat required for reproduction are essential to develop conservation plans for species of concern; however, studying reproduction in wild settings can be challenging, so local data are not always available. The fisher (*Pekania pennanti*) is an elusive carnivore with ties to mature forest features (e.g., cavities, large snags) that occurs across much of boreal North America. This species reaches the southernmost limit of its distribution in the southern Sierra Nevada in a population segment of conservation concern. As data on reproduction and denning habitat in this region are limited, I focused my dissertation on topics related to fisher reproduction in the southern Sierra Nevada, including: 1) reproductive parameters of female fishers here relative to those reported across the species' range, 2) denning habitat relative to resting and available habitat, and 3) attributes of tree cavities used for denning.

In chapter 1, I reviewed literature on fisher reproduction over the species' range for comparison with 7 years of data from the southern Sierra Nevada. On average across its range, 71% of adult females reproduced (range, 40 – 100%; $n = 16$), parturition occurred on 25 March (range, 3 March – 17 April; $n = 16$), and litter size was 2.5 (range, 1 – 4; $n = 16$). In our study area, we tracked 35 of 42 adult female fishers to 257 reproductive dens; 86% (range across years, 79 – 100%) of females attempted denning and 75% (range across years, 64 – 100%) were successful; mean parturition date was 30 March (range 17 March – 12 April; $n = 69$), and mean litter size was 1.57 (range, 1 – 3; $n = 75$). In this region, females reproduced at a rate comparable to or higher than elsewhere, gave birth at similar or later dates, but had the smallest reported litters; I discuss conservation implications of these findings and hypotheses for small litter size.

In chapter 2, I compared fisher use of microsites and structures for resting and denning and assessed habitat selection by denning females at 3 spatial scales. At the microsite scale, both

sexes rested in tree cavities (42.1%), branch platforms (29.7%), broken top platforms (11.1%), burrows (8.4%), and log cavities (7.5%); in contrast, females used tree cavities almost exclusively as both natal (100.0%) and maternal den (99.0%) microsites. At the structure scale, both sexes rested in live conifers (35.4%), live hardwoods (26.3%), and conifer snags (20.1%), while denning females used live hardwoods (51.3%), live conifers (22.5%), and conifer snags (21.3%). Both sexes rested most frequently in white fir (*Abies concolor*), California black oak (*Quercus kelloggii*), and ponderosa pine (*Pinus ponderosa*); denning females used California black oak most often (55.4%), followed by white fir and incense cedar (*Calocedrus decurrens*). Habitat selection analysis suggest that large California black oaks, large snags, dense tree canopy, high stand density indices, decay, slope, and elevation may predict den habitat at different spatial scales.

In chapter 3, we assessed physical and thermal attributes of tree cavities used for denning and spatial attributes of den trees used in a single season by a female (i.e., den cluster). We measured physical traits of cavities used as den microsites (30 natal, 35 maternal); attributes were similar for natal and maternal dens, except that natal den entrances were smaller (mean vertical x horizontal diameter 11.1 x 7.6 cm compared with 19.2 x 9.3 cm). Data from loggers deployed inside and outside previously used den cavities (20 natal, 21 maternal) from late March – June indicate that cavities provided good insulation from cold temperatures. Mean daily minimum temperatures were lower outside than inside cavities for all dens; natal den cavity interiors had a smaller proportion of days with temperatures below 5° C than maternal dens. Within a den cluster, mean distance between trees was 364 m \pm 314 SD (range 0 – 1,894 m) and among all trees was 930 m \pm 650 SD (range 0 – 2,718 m). Spatial attributes of den clusters may reflect a patch size relevant to denning female fishers that would be of use in forest planning.

INTRODUCTION

Concern for the conservation of the fisher (*Pekania pennanti*, formerly *Martes pennanti*) in California was described as far back as 1924 when Joseph Dixon reported that the number of fishers trapped for pelts had been drastically declining; he argued that protection for the species was needed to facilitate persistence of this fur-bearer in the state (Dixon 1924). In 1937, Joseph Grinnell, Joseph Dixon and Jean Linsdale reviewed what was known about the status and ecology of fur-bearing mammals in California; in their chapter on fisher, they expressed concern for the ongoing impacts of trapping for fur and timber harvest. Grinnell et al. (1937) also noted a lack of basic information on reproduction and “breeding dens” for this species in California. In 1942, Raymond Hall provided another summary of the exceptionally low number of fishers trapped annually (relative to earlier years) in the state and strengthened the argument for a closed trapping season by presenting information on the low rate of reproduction in female fishers documented at a fur farm in British Columbia (Hall 1942). In 1946, a ban on lethal trapping of fisher was finally introduced in California, a regulation which is still in place today (Lewis and Zielinski 1996). This trapping ban likely prevented the extirpation of fisher in parts (or possibly all) of California, as occurred elsewhere (e.g., Washington, Aubry and Houston 1992, Aubry and Lewis 2003). Today, new sources of mortality have been documented (e.g., Gabriel et al. 2012, Wengart et al. 2014) while data needed by forest managers to facilitate reproduction in wild fisher populations remain limited, particularly in the southernmost portion of this species’ distribution in the southern Sierra Nevada.

Fishers are closely tied to habitat attributes commonly associated with older forests, including dense canopy cover, large diameter trees, and forest features that can take long periods of time to develop (e.g., large snags, tree cavities; Zielinski et al. 2004, Purcell et al. 2009, Weir

et al. 2012). In the relatively few studies where fisher reproduction has been monitored in wild settings, females gave birth in late winter or early spring in cavities of relatively large diameter trees (Paragi et al. 1996, Weir et al. 2012); females gave birth and cared for young in natal dens, then typically moved their kits to one or more maternal dens over the remainder of the den season (Powell et al. 2003, Matthews et al. 2012). Prior to the initiation of this research project, there were effectively no baseline data on fisher reproductive parameters and very sparse information on the habitat needed to support reproduction in the southern Sierra Nevada. Although information from other geographic areas can provide insights about fisher reproduction in general, the climatic conditions and forest ecosystems in the southern Sierra Nevada are warmer and more xeric than other parts of the fisher's range and tree species differ from those available in study areas further north (Aubry and Raley 2006, Weir et al. 2012) and east (Paragi et al. 1996, Powell et al. 1997). Local data on fisher reproductive ecology were needed to create and implement effective management and conservation plans.

In conjunction with a long-term study of fisher ecology in the southern Sierra Nevada (Kings River fisher project, USDA Forest Service, Pacific Southwest Research Station), I endeavored to address research questions associated with fisher reproductive ecology in this region. My first objective was collect baseline data on fisher reproductive parameters, and assess findings within the context of available information on reproduction from across the species' distribution in North America. My second objective was to characterize the forest habitat used by female fishers during reproduction; specifically, I wanted to compare the microsites and structures used by females for denning with those used by fishers for daily resting throughout the year as well as assess den habitat selection at several spatial scales (structure, site, forest stand). My last objective was to assess physical and thermal properties of tree cavities used by

reproductive female fishers as den microsites, and consider how spatial attributes of trees with cavities used as dens during a single season by a female (i.e., den cluster) could inform conservation and forest management of these large decadent structures. For all objectives, I attempted to design my research protocols in a manner that would yield information of ecological significance as well as applied value for conservation efforts and forest management.

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CHAPTER 1

Fisher (*Pekania pennanti*) reproductive parameters in the southern Sierra Nevada relative to the broader range

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ABSTRACT Quantifying reproductive parameters is essential to develop conservation plans for species of concern; however, because studying reproduction in wild settings can be challenging in many taxonomic groups local data on reproduction frequently are unavailable. The fisher (*Pekania pennanti*) occurs across much of boreal North America and is an elusive forest-dwelling carnivore of conservation concern. This species reaches the southernmost limit of its distribution in the southern Sierra Nevada of California in a population segment that has become geographically isolated. Data on fisher reproduction in this region are limited and the

applicability of parameters from other areas uncertain. To address this, we made a comprehensive review of the literature on fisher reproduction over the species' range, and we compare this with data we collected over 7 years in the southern Sierra Nevada; we emphasize 1) the proportion of females reproducing, 2) parturition date, and 3) litter size. On average across its range, 71% of adult females reproduced (range, 40 – 100%; $n = 16$), parturition occurred on 25 March (total range, 3 March – 17 April; $n = 16$), and litter size was 2.5 (total range, 1 – 4; $n = 16$). In our study area, we tracked 42 adult female fishers, 35 of which used 257 reproductive dens (74 natal, 175 maternal, and 8 apparent failed dens); 0.86 (range across years, 0.79 – 1.0) of our study animals attempted denning and 0.75 (range across years, 0.64 – 1.0) were successful. Mean parturition date was 30 March (range 17 March – 12 April; $n = 69$), and mean litter size was 1.57 (range, 1 – 3; $n = 75$). Hence, female fishers at the southern limit of their distribution reproduced at a rate comparable to or higher than elsewhere in North America, and gave birth at similar or later dates. Average litter size, however, was the lowest reported for the species, suggesting limited capacity to rebound from extrinsic threats. We discuss conservation implications of these observations and explore patterns of variation in litter size across the range relative to climate and body weight.

Key words: den, forest carnivore, litter size, parturition date, *Pekania pennanti*, reproduction

Conservation of rare and declining species can be hampered by a variety of issues including habitat loss (Fahrig 1997), over-harvest (Wittemyer et al. 2014), and disease (McCallum 2012). For rare or elusive species, another common limitation is a lack of basic life history information for planning and modeling efforts; such data include basic natural history, baseline data on

population parameters, and description of habitat for reproduction (Hernandez et al. 2006). Indeed, data on such fundamental reproductive parameters as annual proportion of females reproducing and litter size provide critical insight into the status of a population and its capacity for growth (Barding and Lacki 2014). Identifying local reproductive parameters can inform regional conservation plans, while comparisons across a species' range can generate awareness about reproductive potential or limitations (Garcia and Arroyo 2001, Stock et al. 2015).

Patterns of behavior associated with reproduction and reproductive success may be influenced by both extrinsic (e.g., climate, latitude; Bywater et al. 2010, Lada et al. 2013) and intrinsic factors (e.g., nutrition, body condition, physiology; Sadleir 1969). A species' reproductive timeline may be flexible in the face of variation in temperature (Gladalski et al. 2014), precipitation (Lučan et al. 2013), and food availability (Tomás 2015), or it may be relatively invariant due to physiological constraints (e.g., timing of estrus; Mead 1994) or limitations set by extrinsic factors (e.g., presence of snow cover for reproductive dens of wolverine (*Gulo gulo*), Aubry et al. 2007). Determining the timing of behaviors associated with reproduction can provide important insight to managers and thereby help protect species of concern during critical activities such as parturition, mating, and rearing of young (Kanapaux and Kiker 2013, Webber et al. 2013).

Female mammals in wild settings face many energetic challenges during reproduction, including foraging while pregnant, securing a location to give birth, lactating, and modifying behavioral patterns to raise young (Ofstedal and Gittleman 1989). These challenges may be intensified for mammalian carnivores with large home ranges, strenuous foraging styles, lean body shapes (Brown and Lasiewski 1972), or prolonged periods of offspring care (Laurenson 1995, Miller et al. 2014). Many mustelid carnivores employ delayed implantation, in which a

fertilized egg develops into a blastocyst before entering a period of suspended development (diapause); increasing day length is thought to prompt blastocyst implantation in the uterus, at which time development resumes (Mead 1989, 1994). In mustelids, the length of this delay ranges from 34-37 days in least weasels (*Mustela nivalis*), to 259-276 days in American martens (*Martes americana*), to 327-358 days in fishers (*Pekania pennanti*; Mead 1989).

The fisher is a forest-dwelling mustelid, historically distributed in diverse forest types across boreal North America, with southern montane extensions in the Cascades, Sierra Nevada, Rocky Mountains, and eastern deciduous forests (Graham and Graham 1994, Gibilisco 1994). Fur-trapping in the 1800s and early 1900s led to population declines or extirpations across much of the range (Lewis and Zielinski 1996, Tapper and Reynolds 1996); long-term impacts were most pronounced where trapping coincided with or was followed by extensive timber harvest, as in the western United States (Aubry and Houston 1992, Aubry and Lewis 2003, Zielinski et al. 2005). Concern for the persistence of fishers in California was expressed early in the 20th Century by authors who argued that harvest rates were unsustainable (Dixon 1925, Grinnell et al. 1937, Hall 1942); this ultimately led to a statewide ban on fisher trapping in 1946 which remains in effect today (Lewis and Zielinski 1996). However, new threats to fisher persistence have arisen including potential habitat loss due to extreme fire conditions (Scheller et al. 2011), further geographic isolation of populations (Zielinski et al. 2005), low genetic diversity (Wisely et al. 2004), exposure to rodenticides (Gabriel et al. 2012), and predation by larger carnivores (Wengert et al. 2014). The high energetic demands on female fishers (Powell and Leonard 1983), combined with their lengthy period of delayed implantation, aggravate management challenges for this species, and beg for clearer understanding both of reproductive patterns and environmental requirements.

The collective fisher populations in Washington, Oregon, and California have been classified as a distinct population segment, which was recently considered for listing as threatened under the Endangered Species Act (USFWS 2014); although this listing was not granted, the state of California has classified fishers in the southern Sierra Nevada as an Evolutionary Significant Unit warranting threatened status (CDFW 2015). Extensive surveys in the Sierra Nevada suggest that the distribution of fisher in the southern region has been stable over the last decade (Zielinski et al. 2012), but it has become demographically isolated from other populations (Zielinski et al. 2005) and may have been so since before European settlement (Tucker et al. 2012). Finally, the population size in the southern Sierra Nevada is not well known, but the number of adults may be as low as 125 to 250 individuals (Spencer et al. 2011).

Basic aspects of fisher reproduction remained enigmatic for years; we now know that female fishers enter a brief estrus each year in early spring, and if they mate successfully, implantation of the blastocyst is delayed for nearly 10 months (Mead 1994, Powell et al. 2003). First mating for females can occur at 1 year of age, with earliest parturition at 2 years (Mead 1994). Implantation is believed to be triggered by increasing day length (Pearson and Enders 1943) in association with a peak in progesterone levels in February (documented in captive female fishers; Cherepak and Connor 1992, Frost et al. 1997); subsequent embryonic development takes 36-42 days (Frost et al. 1997). Parturition occurs in late winter or early spring, followed about 7-10 days later by a post-partum estrus and mating (Powell et al. 2003). Females give birth and care for young in structures called natal dens, and they may move kits to a series of 1 or more maternal dens (Powell et al. 2003). Most of this understanding relies on data from populations at more northern latitudes. Prior to the present study few reproductive dens had been found in the Sierra Nevada (Grinnell et al. 1937, Truex et al. 1998); consequently,

local information on reproduction to guide management has been lacking, and the utility of data from more northern regions is unknown. Consequently, improved understanding of fisher reproductive ecology has important management implications, especially in light of conservation concerns outlined above.

We collected comprehensive data on fisher reproduction over 7 years in the southern Sierra Nevada, California. To provide range-wide context for these data, we conducted a comprehensive review of available literature on fisher reproduction. Our primary objectives were to characterize 3 fundamental reproductive parameters at both spatial scales: 1) proportion of females reproducing, 2) parturition dates, and 3) litter size. We hypothesized that the proportion of females reproducing and mean litter size in our study would be comparable to other West Coast populations (Matthews et al. 2013a, Aubry and Raley 2006), but because our site is well south of previously conducted studies we expected parturition dates to be earlier since longer day length at lower latitudes may trigger earlier implantation of blastocysts (Mead 1994). We also investigated whether mean litter size of fisher across the range was correlated with climate variables (temperature, precipitation) as documented by Tökölyi et al. (2014) for a broader selection of carnivores. Finally, we explored the utility of a teat measurement model to estimate local reproduction relative to denning rates (Matthews et al. 2013b) and examined the timing of activities tied to reproduction and kit development, female body weight, and male behavior during the mating period.

MATERIALS AND METHODS

Study site.---We conducted field work from June 2007 through February 2015. Our study area encompassed roughly 43,500 ha of the Sierra National Forest southeast of Shaver Lake,

California, USA (37° 3' N, 119° 11' W), on the west slope of the southern Sierra Nevada, with Yosemite National Park to the north and Kings Canyon National Park to the south (Fig. 1). We focused our research at elevations from 915 to 2,385 m in a region occupied by fishers (Purcell et al. 2009). Most precipitation occurred as rain in the fall and snow in the winter at elevations \geq 1,500 m; precipitation levels were normal during most of the study, but below average in 2013 and 2014 (Mann and Gleick 2015). We refer to our study area as Kings River, as most of the study area lies primarily within the Kings River watershed.

Dominant tree species in elevations encompassed by the study area included California black oak (*Quercus kelloggii*), Canyon live oak (*Q. chrysolepis*), incense cedar (*Calocedrus decurrens*), ponderosa pine (*Pinus ponderosa*), sugar pine (*P. lambertiana*), and white fir (*Abies concolor*). Vegetation within the study area was dominated by lower montane vegetation types, including ponderosa pine-mixed conifer forest, white fir-mixed conifer forest, and giant sequoia (*Sequoiadendron giganteum*)-mixed conifer forest (Fites-Kaufman et al. 2007), and montane hardwood forest (Allen-Diaz et al. 2007). Patches of deciduous forest, meadows, rock outcrops, and montane chaparral (Fites-Kaufman et al. 2007) occurred at middle to high elevations, with mixed chaparral at lower elevations (Keeley and Davis 2007). The USDA Forest Service is the primary local land manager, but some portions are privately owned. Over the last century, management activities on this landscape included timber harvest, prescribed fire, and development (e.g., construction of houses, roads, dams); however, areas of mature forest and patches of large remnant trees are still present. Fire suppression has led to increases in shade-tolerant species and fuels (Fites-Kaufman et al. 2007).

Literature review.---To compile data on fisher reproductive parameters from sources across the species' range we (1) searched digital databases for scientific literature, (2) examined

citations in publications on fisher ecology and reproduction, and (3) contacted fisher researchers personally. Database searches were conducted in Wildlife and Ecology Studies Worldwide and BIOSIS Previews using the terms den, fisher, *Martes pennanti*, *Pekania pennanti*, and reproduction. These searches yielded 54 sources (see Appendices A, B, and C), including peer reviewed journal articles (24), reports (8), theses/dissertations (7), books/book chapters (6), reviews (5), personal communications (2), and fur trade journals (2). If a project was referenced in multiple sources, we included data from only the most relevant reference in a summary.

We reviewed all literature from our search, but focused on sources with clearly interpretable data on the parameters of interest; only sources with sample sizes > 1 individual were included in summaries unless noted, although single observations are mentioned where relevant. The proportion of females reproducing was measured by monitoring dens in the wild, observing females in captivity, studying reproductive tracts of carcasses, and assessing teats of live animals. Parturition dates were documented in captive and wild settings. Litter sizes were counted through den cavity investigations, remote cameras, observations at research facilities and fur farms, and examination of reproductive tracts for corpora lutea, blastocysts, embryos, or placental scars. Because methods and even terminology varied across studies, we suggest standardized terminology related to fisher reproduction, based on prior studies and our experiences, in an effort to clarify interpretation (Table 1).

In many cases, parameter values were not reported by year, making assessment of annual variation impossible or uninformative for comparison in studies with small sample sizes; as such, mean values for parameters were generally pooled across years within a source or reported as presented in publications. As our primary goal was to explore possible geographic patterns, we included nearly all sources available (despite limitations) to assess variation across the range and

identify geographic areas where data are still needed. To generate comparable values of proportion of females reproducing, we identified the number of den attempts relative to den opportunities across the course of a study. Mean parturition dates were typically reported in the source material, but in some cases these were generated directly from source data. Mean litter size was calculated from the number of kits counted relative to the number of litters documented during the study.

We used a paired 1-way *t*-test to evaluate differences between den attempts and successes, and we used 2-way *t*-tests to compare parturition dates and mean litter size in captive versus wild settings. We used a 2-way *t*-test to compare litter sizes from the isolated peninsula in the southwest portion of the range (Oregon, California) with the rest of the fisher's distribution and we employed linear regression to investigate associations between latitude and each reproductive parameter in western North America. Proportional data were transformed using an arcsin transformation prior to analyses.

Latitude serves as a proxy for numerous underlying climatic variables, but the relationships among these may differ across the range of the fisher. Following Tökölyi et al. (2014), we distilled selected climatic parameters using principal components analysis (PCA) for comparison with the 3 reproductive parameters of interest. We selected bioclimatic variables identified as relevant to litter size in carnivores (Tökölyi et al. 2014), and obtained geographically referenced raster data (10-min spatial scale) from WorldClim (Hijmans et al. 2005, www.worldclim.org). As variable descriptions differed slightly between these two sources, we used the terms presented in Tökölyi et al. (2014) and for clarity note the associated WorldClim bioclimatic variable used in analysis: mean annual temperature (Bio1), temperature variability (mean of monthly standard deviations; Bio4), temperature seasonality (difference

between yearly maximum and minimum; Bio7), and mean annual precipitation (Bio12 divided by 12). We overlaid reproductive parameters in ordination space, and assessed relationships among reproductive parameters with informative PC axes using linear regression; the number of informative axes was determined both visually (Scree plot) and with a Monte Carlo randomization (see McCune et al. 2002). We ran separate PCAs for each analysis since the number of sites with data for these reproductive parameters differed.

Trapping and captures in the Sierra Nevada.---We trapped fishers in fall and winter (1 October – 1 March) each year. We occasionally trapped in summer, but success was lower, largely due to interference from black bears (*Ursus americanus*); moreover, juveniles caught before October were too small for radiocollars. We avoided trapping in March – May to preclude catching late-term or lactating females. We captured fishers using live traps (32 x 10 x 12 in, original series model 108, Tomahawk Live Trap, Hazelhurst, WI) affixed with wooden cubby boxes as shelter (Seglund 1995); traps were covered with bark and other natural materials for stability, protection from weather, and camouflage. We baited traps with a chicken leg placed inside a sock which was then hung from the top of the trap between the treadle and wooden cubby. We dabbed a bait lure (Hawbaker's Fisher Lure, Hawbaker and Sons, Fort Loudon, PA or Fisher Red Lure, Proline Lures, Indianapolis, IN) on the sock, and applied a long-distance lure (Caven's Gusto, Minnesota Trapline Products, Pennock, MN or Outreach Call Lure, Proline Lures, Indianapolis, IN) on a nearby tree trunk. During cold periods we placed a piece of fleece (roughly 30 cm x 50 cm) inside the cubby for insulation, and stiff corrugated black plastic (Coroplast, Vanceburg, KY) was placed over the trap to keep the interior dry. Traps were checked each morning, bait was added if eaten or dry (≤ 7 days), and the long-distance lure was refreshed every 3 days.

To facilitate radiocollar attachment, fishers were coaxed out of the trap cubby (by removing a sliding panel), through a thick canvas sleeve, and into a heavy metal handling cone (Seglund 1995). We estimated sex and weight of animals, then sedated them with an intramuscular injection of Ketamine (22.5 mg/kg) mixed with Diazepam or Midazolam (0.125 mg/kg); drugs were administered conservatively, and supplemental injections were given if needed. Once docile, animals were removed from the handling cone, weighed, and gender was confirmed. We applied eye ointment, affixed an eye cover, checked the airway, and monitored temperature and respiration; we maintained body temperature within a safe range (100 – 102°F) while anesthetized using heat packs to warm animals, or rubbing alcohol (applied to underarms and groin) to cool them. Fishers ≥ 1.7 kg were fitted with Holohil radiocollars (model MI-2M, 31 grams, Holohil Systems Ltd., Carp, Ontario, Canada) with a handmade breakaway (Thompson et al. 2012). We used Advanced Telemetry Solutions (ATS) collars (model 1920, 38 grams, ATS, Inc., Isanti, MN) on a few individuals in the first year of the study. Holohil collars weighed $< 2\%$ of body weight while ATS collars were $< 3\%$. Animals were marked with Passive Integrated Transponder (Biomark, Boise, ID) tags inserted subdermally between the shoulder blades. We collected morphological measurements and samples to monitor health (results reported elsewhere).

Fishers were categorized into 3 age groups (assuming a birth date of 1 April) as follows. Juveniles (< 1 year) had very sharp molar cusps, no sagittal crest, and teats of females showed no sign of prior reproduction (nulliparous). Subadults (≥ 1 and < 2 years) showed slight rounding of molar cusps, partially developed sagittal crest (evident in males, none or subtle in females), and teats of females did not indicate prior reproduction (nulliparous). Adults (≥ 2 years) had molar cusps with increased rounding or flattening, defined sagittal crest (pronounced in males, delicate

in females), and the teats of females usually indicated prior reproduction (parous). Teats of nulliparous females typically were very small and the same color as the surrounding skin (white to light pink); in contrast, teats of parous females were slightly larger and generally darker in color (dark pink to brown). Methods were approved by the Institutional Animal Care and Use Committee of the University of California, Davis and correspond with accepted guidelines for mammal research (Sikes et al. 2016).

Model of nipple size vs. reproductive status.---We paired measurements of nipple diameter and height with reproductive history based on den monitoring from the prior season. These data were integrated into a modified version of a model developed by Matthews et al. (2013b) to predict reproductive status of individual females (e.g., confirmed breeder, attempted breeder, non-breeder) from teat measurements. The original model published by Matthews et al. (2013b) included some data from our study area (24 females, 36 occasions) combined with data from 2 other projects in California. We created a revised local model based solely on Kings River fishers which included 3 additional years of data, thereby expanding the occasions for which we could estimate reproductive status; we compared predictions to results obtained from den monitoring. Data were analyzed as in Matthews et al. (2013b) using script provided by the authors and the RandomForest package in program R version 3.2.2 (R Core Development Team 2015).

Den location and monitoring.---We monitored fishers year-round using ground telemetry as part of an ongoing research project conducted by the USDA Forest Service, Pacific Southwest Research Station; occasionally aerial telemetry was conducted through collaboration (see Sweitzer et al. 2015). Beginning in March, we monitored movements of adult females closely (particularly in morning hours) to determine when they localized to an area or structure, behavior

suggestive of parturition. We triangulated to the general vicinity, then homed to resting locations using a hand-held yagi antenna and telemetry receiver (R-1000, Communication Specialists Inc., Orange, CA; Millspaugh and Marzluff 2001, Zielinski et al. 2004). A resting structure located between early March and late June was considered a den if a female used it for ≥ 2 consecutive days, on multiple occasions over a week, or if kits were documented. Once a den was located, we documented use of the structure with as little disturbance as feasible; we monitored remotely with a yagi antenna for several subsequent days and attempted to home in every 4 – 5 days to confirm the female was in the same structure.

We determined litter size each year by investigating den cavities and using remote cameras. If a den tree was safe for climbers, we waited until kits were ≥ 3 weeks old, then ascended the tree to examine the cavity while the female was away from the den (Matthews et al. 2013a). We occasionally observed kits directly, but more frequently we lowered a small security camera connected to a video camera into the cavity to count young and record video for documentation. If the den cavity was low on a structure, we used a camera mounted on a telescoping pole to examine the chamber. We monitored activity of the female during the cavity investigation (with telemetry); if we determined she was returning to her den we terminated efforts and left the area. If den trees were unsafe to climb, cavities were too deep, or tree climbers were unavailable, we set up 1 – 3 remote cameras (Reconyx models PC800, PC85, and PM35T25, Holmen, WI) facing the den tree bole to photograph females moving kits to new dens. Remote cameras provided information on behavior, but sometimes missed kit moves due to slow trigger speed, disturbance (e.g., by black bears), or females using routes out of the camera's view. We tried to balance acquisition of accurate data with potential disturbance, and we monitored females after kit count efforts to ensure that dens were not abandoned. When a count

effort was unsuccessful or we suspected a female moved dens due to researcher activity, we typically waited ≥ 1 week before another attempt. Male visitation to dens was documented through VHF telemetry, remote cameras, and observation of males or tracks in snow at dens.

We investigated the relationship between female weight at capture and denning status (yes/no) at the next possible denning opportunity using a generalized linear mixed model with a logit function fit by maximum likelihood (Laplace approximation) with individual female as a random effect; we evaluated the relationship between female weight and litter size using the same approach. In both assessments, we included only occasions where females would be ≥ 2 years old by the next den opportunity and for which we subsequently knew den status or litter size; in the few cases where females were caught twice between den seasons, we used only the weight from the latter capture. Statistics were conducted in Stata 12.1 (StataCorp 2011), R version 3.2.2 (R Core Development Team 2015), and PC-ORD (McCune and Mefford 2011).

RESULTS

Review of Fisher Reproductive Parameters

Our literature review yielded 54 sources with information on fisher reproduction, of which 36 contained primary data that we included in ≥ 1 summary (Appendix A, B, C). Sample sizes for adult females varied from 1 to 42 on den monitoring studies, 1 to 26 in captive settings, 5 to 94 in projects that assessed teat condition, and 3 to 1173 in examinations of reproductive tracts. Many sources contained data on 1 or 2, but not all 3 parameters of interest (Table 2). Data from the Kings River project (this study) were not included in summaries and associated analysis except where noted to investigate geographic patterns.

Proportion of females reproducing.---The mean proportion of females reproducing ranged from 0.40 to 1.00 across sources using different methods in wild and captive settings (Table 3). Results were influenced by methodology; the estimated mean proportion of females reproducing based on active or recent lactation at captures (0.52; Truex et al. 1998) and on the presence of placental scars in carcasses (0.58; Crowley et al. 1990) were moderate compared to sources using the presence of blastocysts (0.92; Hamilton and Cook 1955, Crowley et al. 1990) or corpora lutea (0.96; Shea et al. 1985, Douglas and Strickland 1987, Crowley et al. 1990) (Table 3). In studies that monitored individual females during parturition (captive and wild settings), the mean proportion of females reproducing was 0.71 ($n = 16$; Table 2, 3). Not all attempts were successful; across 10 sources (including Kings River) where females were monitored in the wild during parturition the subsequent den season, the proportion of females that successfully reared ≥ 1 kit was significantly lower than the proportion that attempted to den ($t_9 = 4.44$, $P < 0.01$; Fig. 2). In sources that monitored females during parturition in western North America, including Kings River, the proportion of females reproducing did not correlate with latitude ($R^2 = 0.05$, $F_{1,8} = 0.43$, $P = 0.53$; $n = 10$) or with dominant axes of a PCA based on bioclimatic variables ($R^2 = 0.06$, $F_{1,13} = 0.79$, $P = 0.39$); this PCA yielded 1 informative axis ($\lambda = 2.89$) that explained 72% of the variance.

Natal den initiation.---Where dates of natal den initiation (wild settings) or parturition (research facilities, fur farms) were recorded, the mean date of parturition (25 March, $n = 16$; Table 3 and Fig. 4) was very similar in wild and captive animals (24 and 27 March, respectively; $t_{14} = -0.82$, $P = 0.42$; Table 3). The range of mean parturition dates was relatively narrow across sources (12 March – 8 April), with a total range in dates from 3 March to 17 April. Mean date of parturition across 9 studies in western states, including Kings River, did not correlate with

latitude ($R^2 = 0.27$, $F_{1,7} = 2.55$, $P = 0.15$) or with dominant axes of a PCA based on bioclimatic variables ($R^2 = 0.06$, $F_{1,9} = 0.61$, $P = 0.46$); this PCA yielded 1 informative axis ($\lambda = 3.11$) that explained 78% of the variance).

Mean litter size.---Estimated mean litter size declined monotonically with developmental stage, being greatest when using counts of corpora lutea (3.3), and declining through counts of blastocysts (3.0), embryos/fetuses (2.8; including Kings River), placental scars (2.8), and live kits post-parturition (2.5; Table 3). Moreover, mean litter size for kits observed in captivity (2.9) was greater than that from wild settings (2.3; $t_{13} = 2.17$, $P < 0.05$). Females in the isolated southwest peninsula of the fisher's range (Oregon and California, including Kings River) had smaller litters than the rest of the range ($\bar{X} = 1.9$ and 2.4 respectively; $t_{14} = -4.56$, $P < 0.01$; Table 2, Fig. 3). Across 8 sites in western North America (including Kings River), litter size was positively correlated with latitude ($R^2 = 0.81$, $F_{1,6} = 2.09$, $P < 0.01$), and in contrast to results for the first two reproductive parameters, mean litter size was significantly associated with the dominant axis of a PCA based on climate variables ($R^2 = 0.61$, $F_{1,11} = 17.18$, $P < 0.01$; Table 4; Fig. 5). This PCA yielded 1 informative axis ($\lambda = 3.27$) that explained 82% of the variance. Positive values on this axis represented sites with warmer mean annual temperatures and higher mean annual precipitation, while negative values reflected sites with greater seasonality and variability of temperature. Hence, sites with greater variability and seasonality of temperature are associated with larger litters, and those with warmer mean annual temperatures and greater mean annual precipitation tended to have smaller litters.

Timing of mating.---While fishers are known to exhibit a post-partum estrus and to mate soon after giving birth, most information on the timing of mating has come from lab studies of male and female physiology and hormone levels (Cherepak and Connor 1992, Frost et al. 1997),

necropsy of carcasses (Enders and Pearson 1943, Wright and Coulter 1967), and behavioral observations in captivity (Hodgson 1937, Frost et al. 1997); we found no published observations of mating in the wild. The most detailed mating records came from fur farms in Canada; Hall (1942) reported 26 observations of mating with a mean date of 12 April (range, 5 – 27 April), and Hodgson (1937) recorded 25 observations of mating with a mean date of 13 April (range, 23 March – 16 May). We know of only 1 visual observation of mating in the wild; as this is such a rare observation, we provide a summary here. While working on a study of fisher reproduction in northwestern California (see Matthews et al. 2013a), one of us (R.E.G.) observed a radiocollared female mating with an uncollared male on the ground 20 m from the female's natal den from 1130 to 1300 hrs. During this observation the pair was quiet and partially hidden by shrubs. This sighting occurred on 20 March 2006, 5 days after the female's natal den was located (personal communication, J. M. Higley, Hoopa Tribal Forestry, Hoopa, CA). Aubrey and Raley (2006) also detected male fishers near active natal dens on several occasions 1 to 2 weeks after parturition, including 1 male resting 5 m from an occupied natal den.

Kings River Trapping and Den Monitoring

Over the duration of our study (June 2007 through February 2015) we trapped 126 fishers on 295 occasions. This included 178 captures of 72 females and 117 captures of 54 males (range, 1 – 8 captures each). We placed radiocollars on 69 females and 54 males, and monitored individual fishers from 2008 through 2015.

Reproductive den sites.---We located and monitored 257 reproductive dens (74 natal, 175 maternal, 8 apparent failed dens) in 237 separate structures used by 35 adult females over 7 denning seasons between March 2008 and June 2014. Twenty of these structures (8.4%) were used either more than once by the same female or by different females in different years. All

dens were located in trees with cavities, except for 2 late maternal dens in hollow logs. During 68 successful denning opportunities that were monitored for a full season, females used an average of 3.5 ± 1.2 dens per year (range, 1 – 7). Three females remained at natal dens for the entire den season, and 3 others reused their natal den structure as a maternal den later in the same season. In 7 of 8 apparent den failures, females localized to a structure for a few days, after which they were not found at the site; the sole exception was a female that revisited 1 tree over a 3-week period. We were unable to confirm kits at these apparent failed dens, but behavior of females was similar to that of known denning females and in 3 cases the structures were used successfully by the same female in another year. We documented 3 confirmed den failures when females were killed by predators while away from their dens; in each case we recovered 1 live kit from a den tree, 1 of which survived long enough to be reared in captivity and successfully released.

Reproductive parameters and observations.---We monitored 42 adult females using telemetry in ≥ 1 denning season, and confirmed 35 females at reproductive dens in ≥ 1 year. Over 7 reproductive seasons we documented 93 den opportunities, 80 den attempts (86%), and 68 den successes (75%; Table 5); the mean proportion of females attempting to den at Kings River across all years (0.86, 95% CI = 0.79 – 0.93) was higher than the mean from our literature review (0.71; Table 3) and greater than 77% of the other studies in Table 2.

Females initiated natal dens (hence, assumed date of parturition) on 69 occasions (across 7 reproductive seasons) between 17 March and 12 April. Excluding 5 cases where access limitations (heavy snow, remote location) delayed discovery of natal dens (≥ 5 days), the mean date ($\bar{X} = 30$ March ± 5.5 days, 95% CI = 29 March – 1 April) was 5 days later than the range-wide mean of 25 March; mean parturition date for Kings River was later than 78% of other

studies in Table 2, although the range of dates from this study and other sources showed considerable overlap (Table 3). Initiation dates for assumed failed dens did not differ from those of successful dens ($t_{75} = -0.29$, $P = 0.77$). Females moved kits from natal to maternal dens between 4 April and 24 June ($\bar{X} = 27$ April, Fig. 6). From 2008 through 2013, our earliest parturition date was 23 March; the spring of 2014 was unusually warm, and this year we recorded our earliest dates for natal den initiation, 1 by a previously reproductive female (17 March) and 1 by a first-time breeder (19 March).

Mean litter size for Kings River (1.57; range, 1 – 3; $n = 75$ litters) was lower than the range-wide mean obtained in the review (2.50, 95% CI for Kings River = 1.44 – 1.71) and less than all other studies reviewed in Table 2. Moreover, litters > 2 were recorded only 3 times by 2 females. One female produced 3 kits in 2 consecutive seasons, but remote cameras indicated that not all kits survived in either year. Another female produced 3 kits, but abandoned 1 at a natal den in May; the kit was in poor condition when found, and died 24 hrs later. In 2 cases we found a dead kit in a den (1 natal, 1 maternal) after a female moved a live kit to a new den.

Model of teat size vs. reproductive status.---We measured teats of 69 females during 150 captures between 2007 and 2015. Our model relating these measurements to the known reproductive status (attempted breeder, confirmed breeder, non-breeder) of 75 females captured in the preceding den season correctly classified 84% of events with known status (Table 6). When we applied this model to teat measurement for another 75 occasions with unknown histories, the model classified 21 animals as breeders and 54 as non-breeders, which generally agreed with observations made during these captures; eighteen of the 21 predicted breeders had been categorized as adults, and 49 of the 54 predicted non-breeders had been identified as juveniles or subadults (Table 6). Using only data from occasions with known or assumed adults

(59 known histories, 26 unknown histories), our model predicted that 75% of females were reproductive.

Female weight and denning behavior.---Mean weights for females across years were 2.17 ± 0.19 kg for adults ($n = 85$ captures, 38 females), 2.05 ± 0.20 kg for subadults ($n = 39$ captures, 39 females), and 2.02 ± 0.17 kg for juveniles ($n = 37$ captures, 37 females). Females that denned successfully at the next opportunity after a capture were heavier than those that did not ($\bar{X} = 2.16 \pm 0.19$ kg, range; $n = 69$ captures, 33 females, vs. $\bar{X} = 1.99 \pm 0.16$ kg, range; $n = 13$ captures, 13 females; GLM, $z_{80} = 2.00$, $P < 0.05$; Fig. 7). Females with apparently failed dens did not differ in weight compared to females with successful attempts (reported above), although sample sizes were small for failed attempts ($\bar{X} = 2.26 \pm 0.15$ kg, $n = 7$ captures, 7 females; $t_{74} = -1.33$, $P = 0.19$). Finally, females giving birth to more young tend to be larger than those having a single kit (1 kit, $\bar{X} = 2.12 \pm 0.19$ kg; $n = 33$ captures, 23 females, ≥ 2 kits, $\bar{X} = 2.20 \pm 0.19$ kg; $n = 36$ captures, 24 females; GLM, $z_{67} = 1.74$, $P = 0.08$). For this comparison we combined females with 2 or 3 young since we have very few of the latter; however, females with 3 kits showed a slight tendency to be heavier than those with 2 (Fig. 7).

Males were detected visiting natal dens between 29 March and 6 May (Fig. 6), with most visits in the first half of April when females were likely to be in estrus. Information related to fisher mating in the wild is scarce, so we describe several observations here, recognizing that the link between observations and mating is circumstantial in some of these. (1) On 6, 8, and 10 April 2008, we located 3 radiocollared males at the same California black oak on separate days; based on this highly unusual behavior, we suspected the tree was an active natal den, so on 10 April we set up remote cameras. On 16 April we detected an uncollared female-sized fisher carrying a kit. (2) On 6 April 2010, R.E.G. observed a male fisher on the trunk of a natal den; he

sniffed at the cavity entrance where a female was concealed, then left. On 13 April 2011, R.E.G. visually observed a different male resting on a platform in the same natal den tree while the same female was in the cavity; in both instances males were suspected to be waiting for the female to exit the den chamber. (3) On 2 April we set up a remote camera at a natal den that had been discovered on 26 March 2012; on 6 April 2012 we photographed a male chasing a female up the tree, grabbing her by the scruff of the neck, then mating at the base of the tree. (4) On 26 March 2013, we found the carcass of a large male fisher freshly killed by a predator within 30 m of an occupied natal den at a time when the female was likely in estrus. (5) On 30 March 2014 while tracking a 2-year old female, R.E.G. observed tracks of 2 fishers in the snow going the same direction, sometimes side by side, for about 200 m; she saw the female resting in a tree with a larger fisher (presumably male, uncollared). This female initiated a natal den a year later (28 March 2015). In addition to these sightings, we observed males at natal dens on 8 other occasions; males typically left as researchers approached, but sometimes stayed in the den tree.

Our remote cameras documented females moving kits from dens, 1 at a time by the scruff of the neck, during both daylight and nighttime hours ($\bar{X} = 1130$ hrs, $SD \pm 6.3$ hrs, range, 0100 to 2256 hrs). Females with multiple offspring moved all kits within a relatively short period (mean time between moving kits = 33 min., $SD \pm 23$, range 13 to 76 min; $n = 11$); an exception to this pattern (not included in the mean value) was an individual female that waited nearly 24 hours before moving the second of 2 kits. Kits were first photographed outside den cavities, clinging to tree trunks with limited coordination, between 8 and 15 June; some kits were not photographed outside prior to 3 July. Through late June, we obtained photographs of females assisting semi-mobile kits down den trees to the ground by grabbing the scruff of their neck. By late June to early July kits moved with greater coordination, but still lacked the agility of adults.

From July through September, we located reproductive females at maternal rest structures (rest sites used by females with mobile kits post-den season) such as hollow logs (Fig. 6), stumps, trees with low cavities, and rock or burrow chambers. In June and July, females appeared to hide kits at maternal rest sites while they foraged, then brought prey back; these sites were sometimes used for multiple days or returned to at later dates. The latest we photographed a female bringing prey back to 2 kits at a maternal rest site (a hollow log) was 21 September.

DISCUSSION

Reflecting the boreal distribution of fishers, most research on their reproductive biology comes from higher latitudes. Environmental conditions at the southern end of this species' distribution are quite different, however, and may select for different reproductive strategies, leaving resource managers uncertain as to the reliability of available (e.g., largely boreal) data for local management. Prior to our study and those of a complementary effort nearby (Sweitzer et al. 2015), information on fisher reproduction in the southern Sierra Nevada was extremely limited; these studies offer the first detailed reports of reproductive parameters in the southernmost portion of the fisher's distribution. In this report we integrate novel information with findings from a comprehensive review of literature to highlight similarities and differences in reproductive parameters across their range. We focused on 3 key parameters and our results shed light on potential limitations to reproductive output by fishers. Specifically, the proportion of female fishers attempting to reproduce each year in the southern Sierra Nevada is higher than that reported elsewhere in western North America, but litter sizes in our study region represent the lowest reported for the species. Contrary to our expectations of earlier parturition dates in the southern Sierra Nevada, we found parturition dates to be similar to or later than more

northern areas, suggesting that factors other than (or in addition to) total day length influence this parameter. We consider conservation implications of our summary of reproductive parameters and discuss findings about fisher reproductive ecology from the southern Sierra Nevada.

Proportion of females reproducing.---Different methods have been used to assess reproduction in female fishers, and some reflect potential rather than confirmed reproduction. Because not all ova will be fertilized and not all blastocysts will result in kits, primary measures of reproductive activity (e.g., counts of corpora lutea or blastocysts) can yield inflated estimates of reproduction (Crowley et al. 1990). The most meaningful measure of reproduction for conservation is the proportion of females producing viable kits in the wild and this is best obtained by monitoring dens. Based on studies from our literature review where individuals were monitored during parturition, the overall mean proportion of adult females showing signs of reproduction in the wild was moderately high (72%), but dropped to 59% where success could be determined. Data from our study area show that both the proportion of females attempting to reproduce (86%) and the proportion that did so successfully (75%) exceeded these range-wide mean values. These results are comparable to other long-term studies in California (Matthews et al. 2013a, 87% and 65%, respectively; Sweitzer et al. 2015, 85% and 75%, respectively); in contrast, a study in Oregon indicated lower values (Aubry and Raley 2006, 55% and 40%, respectively). Due to limitations with available data, we were unable to assess annual variation in female reproduction across sources; as more long-term studies of fisher reproduction are completed, comparisons which include geographic and annual variation could be informative.

Can reproduction be estimated with teat measurements?---Estimates of reproductive activity based on teat measurements were not entirely independent, as den findings contributed to the initial model creation, but results reported here reinforce Matthews et al. (2013b) in

suggesting that teat measurements provide an acceptable alternative to den monitoring if local models are created. In our project, 96% of females estimated to be < 2 years old were classified as nonbreeders by the model, which corresponded with results of our den monitoring efforts and aging criteria, and the estimated proportion of females reproducing at Kings River based on teat measurements (75%) was equivalent to the measure of females reproducing successfully based on den monitoring (75%). In past studies, fishers have been trapped during the denning season; now that less invasive methods are available, we caution against this practice as it increases risk to kits and disrupts activities of denning females (Coulter 1966, Leonard 1986, Arthur and Krohn 1991). Moreover, teat measurements may reduce the subjectivity inherently associated with a visual assessment of recent lactation; this may explain the lower percentage of females characterized as reproductive in our study region by Truex et al. (1998).

Parturition dates.---In contrast to our prediction, parturition did not occur earlier at lower latitudes; instead, populations at middle latitudes (northern California, Oregon, Maine) generally had earlier parturition dates than those further north (British Columbia) or south (Sierra Nevada). Moreover, fishers in our study gave birth later than the range-wide mean (30 vs. 25 March), not earlier as per our prediction; we question whether this brief period is biologically important, but it underscores the potential importance of factors other than total day length in prompting blastocyst implantation and subsequent development. The range of mean parturition dates was notably limited in our literature review (12 March – 8 April), and is not greatly different from the range of dates observed in our study (17 March – 12 April) suggesting a distinct birthing period for this species as well as further eroding the ecological significance of the later parturition date documented here. Interestingly, the earliest documented parturition date of 3 March occurred in captivity the day after a female had been caught in the wild, although this may have been

influenced by trap-related stress (Coulter 1966). Although methodology may have influenced reported parturition dates (e.g., a function of limited access, variation in resources or technician experience), recent studies generally have employed rigorous protocols, and we believe that most natal dens were generally found within a few days of initiation.

Increased light exposure is thought to be the primary trigger for blastocyst implantation. This is associated with longer total day length at southern locations and with larger increments of increasing daylight at northern sites; however, the limited variation in parturition dates across nearly 19 degrees of latitude suggests other factors may also influence this event (Mead 1989). For example, the closely related pine marten (*Martes martes*) give birth about a week later in years with low prey abundance (Kleef and Wijsman 2015). Powell et al. (2003) noted that some female fishers giving birth around the same date each year. The latter authors suggested that individual patterns might contribute to the overall variation in parturition dates. Further investigation of long-term data sets in multiple geographic areas could assess possible influences of multiple factors on parturition dates and evaluate the plasticity of these dates within individuals and populations.

Litter size.---Relatively few sources provide data on fisher litter size, especially in wild settings; additionally, sources were not distributed evenly across the range, and available data included both captive and wild fishers. From these data, however, fishers appear to have relatively low litter sizes compared to some generalist carnivores like striped skunk (*Mephitis mephitis*; Wade-Smith and Verts 1982) or coyote (*Canis latrans*; Sacks 2005), but are within a comparable range for related species (Mead 1994). Litter size data for related species within the *Martes* complex (Proulx and Aubry 2014) are limited; however, available information puts the range-wide mean litter size of fisher (2.5) just below values for the smaller-bodied pine marten

(*Martes martes*, mean 2.8, range 1 – 5; Wijsman 2012) and the American marten (*M. americana*, mean 2.9, range 1 – 4; Erb et al. 2014), but slightly above values for the larger-bodied wolverine (mean 1.9-2.0, range 1 – 4; Magoun and Copeland 1998, Persson et al. 2006). Moreover, the lowest litter size estimates among fisher populations come from the southern Sierra Nevada (1.57 from this study; 1.6 from Sweitzer et al. 2015). We are confident that the low value in our study represents a real difference because we had a large sample size, obtained comparable counts with complementary methods for some of the same litters (tree climbing and remote cameras), and we made repeated attempts to count young if initial efforts appeared unclear. Uncertainty of counts at cavities occurred if the den chamber was too deep, a feature of the cavity prevented a clear view of the chamber floor, or kits were partially buried in wood chips; uncertainty of counts in photos typically occurred if the image was blurry (e.g., female moving too fast), the female's mouth was out of view (e.g., only hind end visible), or the female was photographed going back up the tree after moving 1 kit, but not coming back down.

As with other metrics, methodology likely influences litter size estimates; estimates obtained from counts of corpora lutea and blastocysts tended to overestimate the number of kits born, while counts of placental scars (Crowley et al. 1990) were comparable to den monitoring values. Counts of kits from wild dens and captive settings may best reflect the number of young produced per female, although counts conducted early may overestimate the number surviving to later stages. In our review and field study, we estimated litter size from kits produced without subtracting losses because (outside of captivity) mortalities were only found opportunistically, but certainly kit mortality occurs. Frost and Krohn (1997) reported that of 38 kits born to 16 captive females, only 28 survived the first week and 23 survived the first year. York (1996) and

our study each documented 3 cases where females left kits (both live and dead) behind when moving to new dens, and Matthews et al. (2013a) noted that 6 kits died prior to weaning.

Our results indicate that fishers tend to have larger litters in areas with greater seasonality or variability in temperatures (often at higher latitudes) and smaller litters in areas with warmer mean temperatures and greater mean precipitation (Fig. 4). These observations agree with those of Tökölyi et al. (2014) who suggested that larger litters in areas with harsh winters may be a strategy to compensate for high winter mortality; the complement to this hypothesis would be a higher survival rate of young in areas with milder winters. At range extremes, however, animals may already be at or near their thermal tolerance limits, and the extent to which increased overwinter survival may be matched or exceeded by increased summer mortality is not clear. In western states, global climate change is predicted to lead to warmer temperatures and proportionally more rain relative to snow; in the Sierra Nevada we expect earlier snowmelt and drier late summer/fall conditions (Rauscher et al. 2008, Ashfaq et al. 2013). Fishers may have some ability to cope with warmer temperatures through behavioral adaptation (e.g., selection of cool microsites for resting, increased foraging activity at night), but persistently dry conditions during hotter summer months could impact fishers directly by limiting availability of free water and cool microclimates (e.g., in riparian areas), and indirectly by limiting productivity in forest ecosystems (e.g., tree growth, prey abundance); at what point changes in climatic conditions would affect fisher survival is currently unknown.

Alternative explanations for small litter size include diet limitations, smaller body size, and limited genetic diversity. The fisher diet in the Sierra Nevada differs notably from that in other geographic areas. Whereas snowshoe hare (*Lepus americanus*) and porcupine (*Erethizon dorsatum*) are key elements over much of the range (Martin 1994), these are largely unavailable

in the southern Sierra Nevada (Zielinski and Duncan 2004); instead, fishers subsist on relatively small and more diverse items, including squirrels, birds, carrion, fruit, lizards, and insects (Zielinski et al. 1999, Zielinski and Duncan 2004). Mean weight of adult female fishers in our study area ($\bar{X} = 2.17$ kg, $SD \pm 0.19$; $n = 85$ captures) was lower than reported for females further north (Maine, $\bar{X} = 2.3$ kg, Frost et al. 1997; British Columbia, $\bar{X} = 2.7$ kg, Weir and Corbould 2008; Oregon, $\bar{X} = 2.85$ kg, Aubry and Raley 2006). This may be a function of Bergmann's Rule (Freckleton et al. 2003), and may benefit these animals under warmer conditions while amplifying thermal challenges associated having a slender mustelid body form (Brown and Lasiewski 1972, Powell et al. 2003). How this tradeoff will influence fisher survival may depend on how climate changes in this region. Fishers may have reached the Sierra Nevada only within the last 5000 years (Wisely et al. 2004), and populations in the southern Sierra Nevada may have become isolated from other fisher populations before the arrival of European Americans (Tucker et al. 2012). Both demographic expansion and long-term isolation could lead to limited genetic diversity, and Wisely et al. (2004) showed that West Coast fisher populations have lower genetic diversity than populations in the core of this species' range, with allelic richness lowest within populations of the southern Sierra Nevada. Whether reduced genetic diversity has impacted fisher reproduction in this region is unknown, but this can be a concern in relatively small and isolated populations (Lacy 1997).

Additional Findings and Conservation Implications

The literature includes little documentation of male behavior related to mating in wild settings; hence, our limited information on this topic may be of particular value. Our observations of male fishers at or near natal dens after parturition, combined with those of Aubry and Raley (2006), suggest that natal dens may play a larger role in coordinating mating than previously

thought. Fisher home ranges are large and the mating period is brief; our observations suggest that males may increase their chances of mating by waiting near or traveling by active natal dens. We documented males resting on branches, climbing trunks, and mating near natal dens, but saw no indication that they enter den chambers; they may simply be too large to do so. These observations suggest den site selection may provide females with some choice in mate selection, although this likely is reduced when they are outside the den. The mating period appears to be energetically expensive and potentially hazardous for males due to extensive travel, exposure to predators while waiting for females, and vulnerability when mating on the ground; conservation plans could incorporate connectivity between areas of suitable denning habitat to promote safe travel for males and facilitate mating.

In considering impacts of management activities on reproductive female fishers and kits, the denning season and summer kit rearing period may be best viewed as a continuum along which the activities of females change and the needs and vulnerabilities of kits vary as they increase in size and mobility, shift from milk to solid food, and develop skills to become independent. The likelihood of a specific management activity having a negative impact on reproduction may vary depending on the stage of kit development and the proposed action. Most females in our study appeared to stop using specific den structures by mid- to late June; however, after the denning period semi-mobile but naïve kits could still be negatively impacted by activities that separate them from their mother or cause physical damage to structures where they are hidden (e.g., hollow logs, ground burrows). Based on photographs from our remote cameras at dens and maternal rest sites, kits develop climbing skills and agility gradually and individual kits appear to progress at different speeds. Kits also appear to rely on the female for food through most of the summer, so kits separated from their mother too early may not survive;

observations from captivity (Coulter 1966) and our remote cameras suggest that females may continue to nurse kits (to some extent) into early summer even after the kits have started eating solid food. In late June and July, we photographed females leaving kits at structures with low entrances, then returning with prey, suggesting that kits were not sufficiently agile to accompany the female. By August, photos and observations suggest kits were traveling with the female. We have limited data on timing of kit independence, but we photographed 1 female bringing prey to 2 kits in late September, and another female traveling with a kit in early October; these observations attest to the substantial investment of time and energy required to rear fisher kits.

Grinnell et al. (1937) was one of the first to suggest that a relatively low reproductive rate may limit fisher population growth; this was reinforced by Hall (1942) who provided some of the first published records of fisher reproductive parameters. Fisher reproduction in the southern Sierra Nevada reflects that of other geographic areas overall, but with some important local differences. Small litter size in this region may be partially offset by the relatively high proportion of females reproducing, but if the population declines fewer females may be available to support demographic recovery. Perhaps the most important result of this study is that reduced litter size may be a reproductive parameter of particular management consideration. Moreover, disturbances in late March and April have the greatest probability of impacting fisher reproductive success as this is the critical time when parturition for the current year as well as mating for the subsequent year occur, and kits may be especially vulnerable due to their small size combined with cold temperatures common in the mountains in early spring.

Existing data on fisher reproductive biology are heterogeneously distributed. Further work should aim to provide baseline data in areas where these aspects of fisher ecology have not been studied (e.g., Adirondacks, Rocky Mountains, south-central Canada) and ideally include

multiple years to capture annual variability. Additionally, further work should also aim to characterize the relationship between prey availability, composition, and fisher reproduction, and to assess survival of juveniles relative to litter size. In the southern Sierra Nevada specifically, further work is needed to characterize the habitat required by reproductive female fishers. Finally, the specter of climate change looms over all boreal species whose ranges extend south in montane regions; further work should strive to better understand how climate change will influence survival in winter as well as through potentially drier summer seasons.

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Table 1. Proposed standardized terminology and suggestions for use in studies of fisher reproduction. Terms and descriptions are based on research in the *Martes* complex and experience of the authors in studying fisher reproductive ecology in western North America.

Term	Description
Reproductive female	A female that shows signs of reproduction, demonstrated by locating a reproductive den, by anatomical changes (e.g., teat measurements), or by observing or photographing her in the presence of kits.
Proportion of females reproducing	The number of adult females (≥ 2 years) showing signs of reproduction during a defined time period divided by the number of adult females monitored or assessed. To facilitate comparisons, the time frame (e.g., year, years), method (e.g., den location, teat measures), phase of reproduction (e.g., ovulation, pregnancy, parturition, denning), setting (e.g., wild, captive, wild trapped carcasses), and age class (juvenile, subadult, adult) should be clarified.
Denning rate	The proportion of females initiating natal dens relative to the number of females monitored in a wild setting that were old enough (≥ 2 years) to give birth (e.g., Matthews et al. 2013a).
Den opportunity	For an individual female fisher, each spring den season during which she is an adult (≥ 2 years) and sufficiently monitored to assess reproductive status (e.g., Powell 1993, Matthews et al. 2013a). Opportunities can be tallied across multiple animals or multiple years to make general comparisons across studies, recognizing that patterns of individual variation or annual variation may be diluted. Number of individual females should be noted.
Den attempt	A den attempt is an opportunity during which a female exhibits signs of parturition by localizing to one structure on ≥ 2 sequential days or multiple days in a week in early spring.
Den success	A den success in a den opportunity during which a female produces and rears ≥ 1 kit through a full den season. The den season ends as females discontinue localization at individual structures for extended periods, kits begin eating solid food, and kits increase in mobility.
Apparent den failure	An apparent den failure is an attempt in which a female appears to localize to a natal den for at least a few days, then stops attendance. Den initiation and failure are based on behavior patterns, not observation of kits, resulting in some uncertainty about whether kits were born.
Confirmed den failure	A den attempt in which a female initiates a den but either she dies, her kits die, or the litter is abandoned. Kits (live or dead) are confirmed after the female dies or stops attendance.

Reproductive den	A reproductive den is the location used by a reproductive female as a refuge to conceal herself and her kits while they are young, vulnerable, and typically still nursing during spring and early summer. Den structures generally are live trees or snags with microsites (cavities) large enough to hold a female with kits. A reproductive den can be either a natal den (where parturition occurs) or a maternal den (structures subsequent to the natal den).
Parturition date	The date when a pregnant adult female gives birth. In field studies, parturition is assumed to occur when a female first localizes to a natal den; the date is estimated based on den attendance behavior not observation. In captivity, females typically retreat into nest boxes.
Litter size	The number of kits produced by an individual female in a given year. To facilitate comparisons, noting the time frame of counts and methods is useful. If information on kit mortality or survival in the den season is known, a late season litter size can be estimated.

Table 2. Sources with data on reproductive parameters from across the range of fisher in North America. Only sources in which individual females were monitored during parturition were included. ID denotes site locations indicated in Fig. 3.

ID	State or Province	Den Seasons	Setting ¹	Proportion Reproducing (<i>n</i> = den opp.)	Parturition Date (<i>mean/median*</i> , <i>n</i> = occasions)	Litter Size (<i>mean, range</i> , <i>n</i> = litters)	Source
A	CA	7	W	0.86 (93)	30 Mar (69)	1.57 (1-3; 75)	Green et al., this study
B	CA	6	Wild	0.85 (73)	28 Mar (62)	1.6 (1-3; 48)	Sweitzer et al. (2015)
C	CA	3	R-Wild	0.92 (12) ²			Facka et al. (2016)
D	CA	2	Wild	0.53 (19)	28 Mar (2)		Self and Callus (2006), James et al. (2008)
E	CA	7	Wild	0.87 (90)	22 Mar (22)	1.9 (1-3; 28)	Matthews et al. (2013a)
F	OR	2	Wild	0.83 (6)	23 Mar (2)	2.3 (1-4; 6)	Clayton (pers. comm.)
G	OR	7	R-Wild	0.55 (20)	26 Mar (11)*	1.9 (1-3; 8)	Aubry and Raley (2006)
H	WA	3	R-Wild	0.40 (5) ²			Facka et al. (2016)
I	BC	6	Fur Farm		31 Mar (22)	2.7 (1-4; 26)	Hall (1942)
J	BC	3	Wild	0.69 (18)	4 Apr (12)		Weir and Corbould (2008)
K	BC	2	Wild			2.8 (2-4; 5)	Simpson et al. (2013)
L	BC	5	Wild	0.85 (31)	28 Mar (16)	2.4 (2-3; 12)	Weir 2009, Weir (pers. comm.)
M	MB	na	Captive		8 Apr (2)	2.0 (1-3; 2)	Cherepak and Connor (1992), Cherepak (1993)
N	MB	1	Fur Farm		4 Apr (2)	3.4 (10)	Douglas (1943)
O	MB	2	Captive, Wild	1.00 (1,1)	28 Mar (1)	≥3.0 (≥2-4;1,1)	Leonard (1986)
~	ON	4	Fur Farm		25 Mar (9)	2.9 (8)	Hodgson (1937) –no location
P	MN	7	Wild	0.78 (51)		2.5 (1-4; 37)	Erb et al. (2013)
Q	MN	na	Captive	0.50 (2)	29 Mar (1)	2.0 (1)	Powell (1977)
R	MA	3	Wild	0.68 (28)	17 Mar (20)*	2.83 (2-4; 19)	York (1996), Powell et al.(1997)
S	ME	4	Wild	0.83 (6)	21 Mar (12)*	2.5 (1-3; 5)	Paragi et al. (1994, 1996)
T	ME	3	Wild	0.62 (13)	18 Mar (6)*		Arthur and Krohn (1991)
U	ME	na	Captive		12 Mar (2)	3.0 (2)	Coulter (1966)
V	ME	3	Captive	1.00 (14)	24 Mar (14)	2.7 (1-4; 14)	Frost and Krohn (1997)
W	ME	3	Captive	0.53 (17)			Frost et al. (1997)

¹ Captive (wild caught or captive born females kept for research in outdoor pens), Fur Farm (wild caught or captive born females kept in outdoor pens for fur production), Wild (wild caught females monitored in the same wild setting), R-Wild (wild caught females associated with a translocation, monitored in the wild)

² Only values for females released early during translocation are noted and used in summaries; values for females released late were 0.38 (CA) and 0.11 (WA; Facka et al. 2016).

Table 3. The results of our review of 3 key reproductive parameters from available sources using different approaches across distribution of fisher paired with our findings from the Kings River Fisher Project in the southern Sierra Nevada.

Parameter and Approach	Literature Review Mean \pm <i>SD</i> (range of means; <i>n</i> = no. of sources)	Kings River Mean (\pm annual <i>SD</i> , range across years; <i>n</i> = den opportunities or occasions)
Proportion of Females Reproducing		
Monitoring during parturition		
(wild)	0.72 \pm 0.16 (0.40 – 0.92; 13)	0.86 \pm 0.07 (0.79 – 1.00; 93)
(captive)	0.68 \pm 0.28 (0.50 – 1.00; 3)	
(combined)	0.71 \pm 0.18 (0.40 – 1.00; 16)	
Den attempts	0.78 \pm 0.13 (0.55 – 1.00; 10)	0.86 \pm 0.07 (0.79 – 1.00; 93)
Den successes	0.59 \pm 0.14 (0.40 – 0.83; 10)	0.75 \pm 0.13 (0.64 – 1.00; 93)
Evidence of lactation	0.52 (0.50 – 0.53; 2)	
Corpora lutea (presence)	0.96 \pm 0.01 (0.95 – 0.97; 3)	
Blastocyst (presence)	0.92 \pm 0.15 (0.83 – 1.0; 2)	
Placental scar (presence)	0.58 (1)	
Parturition Dates		
(wild)	24 Mar \pm 5.2 (17 Mar – 4 Apr; 10)	30 Mar \pm 5.5 (17 Mar – 12 Apr; 76)
(captive)	27 Mar \pm 8.7 (12 Mar – 8 Apr; 6)	
(combined)	25 Mar \pm 7.1 (12 Mar – 8 Apr; 16)	
Litter Size		
Kits produced		
(wild)	2.3 \pm 0.4 (1.6 – 2.8; 9)	1.57 \pm 0.2 (1 – 3; 75)
(captive)	2.8 \pm 0.5 (2.0 – 3.4; 6)	
(combined)	2.5 \pm 0.5 (1.6 – 3.4; 16)	
Corpora lutea (counts)	3.3 \pm 0.4 (2.7 – 3.7; 8)	
Blastocyst (counts)	3.0 \pm 0.1 (2.9 – 3.1; 4)	
Embryo/Fetus (counts)	3.1 \pm 0.2 (3.0 – 3.3; 2)	2.0 (1; 1)
Placental scars (counts)	2.8 \pm 0.2 (2.7 – 2.9; 2)	

Table 4. Results of the first 2 principal component axes based on climate variables from sites with data on three fisher reproductive parameters: proportion reproductive, parturition date, and litter size. Both a scree plot and a Monte Carlo randomization test indicate that only the first axis is informative. Interpretation of PC1 was similar across parameters, but only litter size showed a significant relationship with PC1. We present the second axis to complement the bivariate diagram in Fig. 5.

Variance and Variables	Eigenvectors					
	Proportion Reproductive		Parturition Date		Litter Size	
	PC1	PC2	PC1	PC2	PC1	PC2
Variable						
Mean annual temperature	0.424	0.713	0.526	0.223	0.532	0.213
Temperature variability, monthly SD	-0.563	-0.144	-0.523	0.419	-0.523	0.387
Temperature seasonality, annual max - min	-0.560	0.168	-0.516	0.439	-0.509	0.469
Mean annual precipitation	0.435	-0.665	0.429	0.763	0.429	0.765
Eigenvalues	2.887	0.744	3.226	0.653	3.27	0.65
Explained variance (%)	72.17	18.59	80.64	16.31	81.74	16.33

Table 5. Results of fisher den monitoring on the Kings River study area across 7 reproductive seasons (2008 – 2014). See Table 1 for definition of key terms. Standard deviation was generated from annual data and represents some degree of annual variation.

Metric Associated with Fisher Reproduction	2008	2009	2010	2011	2012	2013	2014	Total	Mean (\pm <i>SD</i>)
Den opportunities	7	16	15	11	14	20	10	93	13.3 (\pm 4.3)
Den attempts	7	14	13	9	11	18	8	80	11.4 (\pm 3.9)
Den successes	5	11	12	7	9	16	8	68	9.70 (\pm 3.6)
Assumed failed dens	0	2	0	2	2	1	0	7	1.00 (\pm 1.0)
Females with kits that died during the den season	0	1	1	0	0	1	0	3	0.40 (\pm 0.5)
Unknown fate of dens due to collar loss	2	0	0	0	0	0	0	2	0.30 (\pm 0.8)
Proportion of adult females attempting to den	1.00	0.88	0.87	0.82	0.79	0.90	0.80	–	0.86 (\pm 0.07)
Proportion of adult females with successful dens	1.00	0.69	0.80	0.64	0.64	0.80	0.80	–	0.75 (\pm 0.13)
Parturition date (mean)	4/8	3/27	4/3	4/3	3/30	3/29	3/25	–	3/30
Parturition date (\pm SD in days)	\pm 5	\pm 3	\pm 5	\pm 6	\pm 5	\pm 4	\pm 6	–	\pm 5
Fisher kits counted	10	18	22	19	12	26	11	118	–
Litters counted	7	12	13	10	9	17	7	75	–
Litter size produced (mean value)	1.43	1.50	1.69	1.90	1.33	1.53	1.57	–	1.57 (\pm 0.2)

Table 6. Contingency table showing observed and predicted classifications of reproductive status for 75 adult female fishers from the Kings River study, based upon a combination of field data collected on teat measurements, reproductive status, and a random forest model developed by Matthews et al. (2013b). The model, in conjunction with age estimates from captures, predicted reproductive status for the 75 occasions with unknown histories. Numbers in bold denote correct classifications by the model.

		Pred.		
		Attempted Breeder	Confirmed Breeder	Non-Breeder
Obs.	Attempted Breeder	0	2	1
	Confirmed Breeder	0	43	9
	Non-Breeder	0	0	20
	Unknown Status	0	21	54
Total		0	66	84

Figure 1. Location of the Kings River study area relative to (a) the Sierra National Forest and adjacent National Parks in California's Sierra Nevada, and (b) local landmarks near Shaver Lake. The light gray shading in (b) denotes a 1 km buffer around trap locations (2007 – 2014) and the primary area of fisher monitoring. Topography in the area is steep and elevations range from 910 to 2390 m.

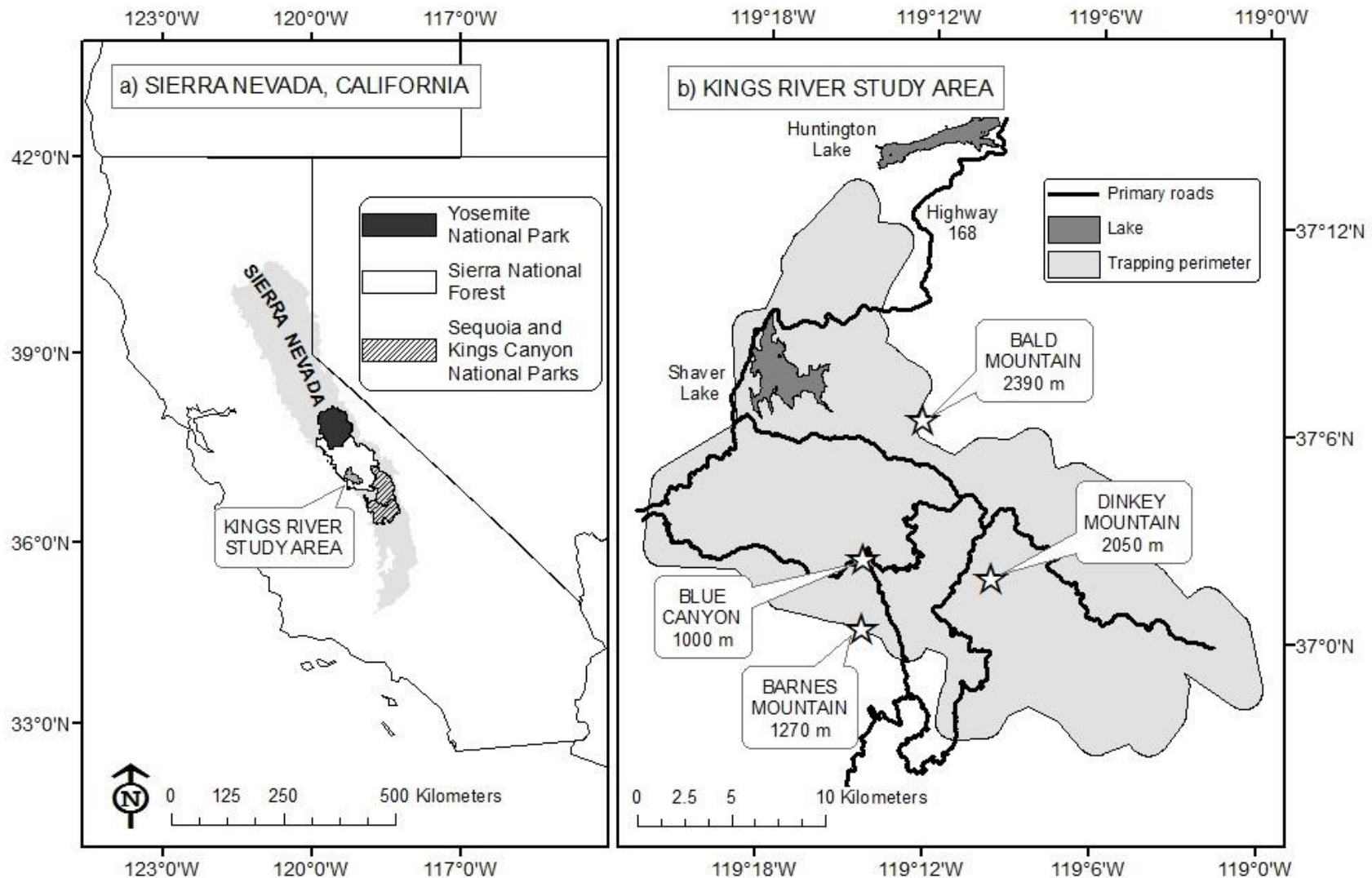


Figure 2. Relationship between the number of den opportunities, attempts, and successes in 10 studies where adult female fishers were monitored during parturition and through the den season in wild settings across North America. The proportion of adult females attempting to den was generally high across studies, although not all females that attempted to den were successful.

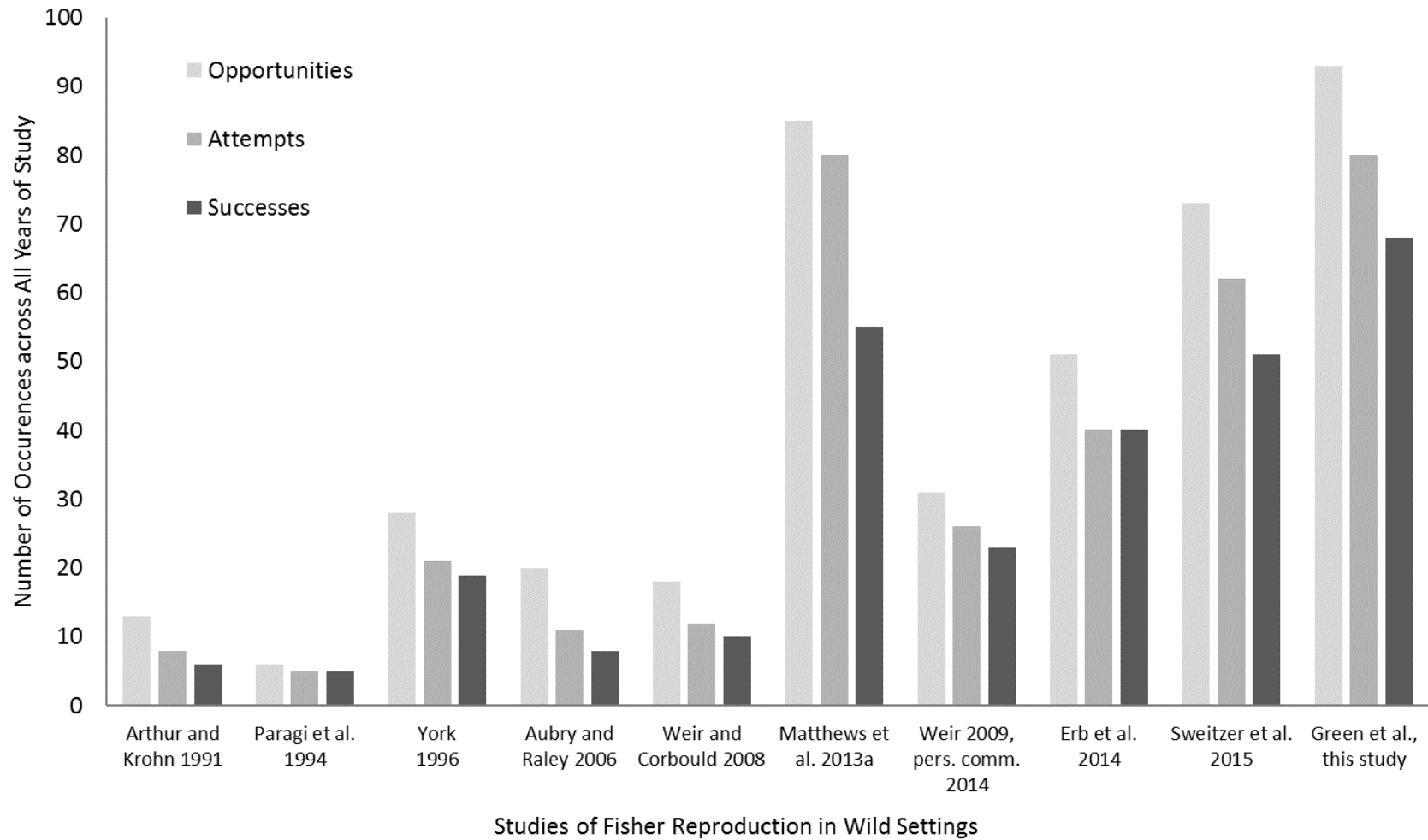


Figure 3. Distribution of fisher mean litter sizes studies in North America and sources where ≥ 1 female fishers were monitored during parturition. Lettered sites indicate locations where data were collected on ≥ 1 fisher reproductive parameter (see Table 2 for references). The dashed black line denotes the historic range of fishers based on Gibilisco (1994). Gray shading shows annual range of temperatures (maximum – minimum) based on spatial data from WorldClim (Hijmans et al. 2005).

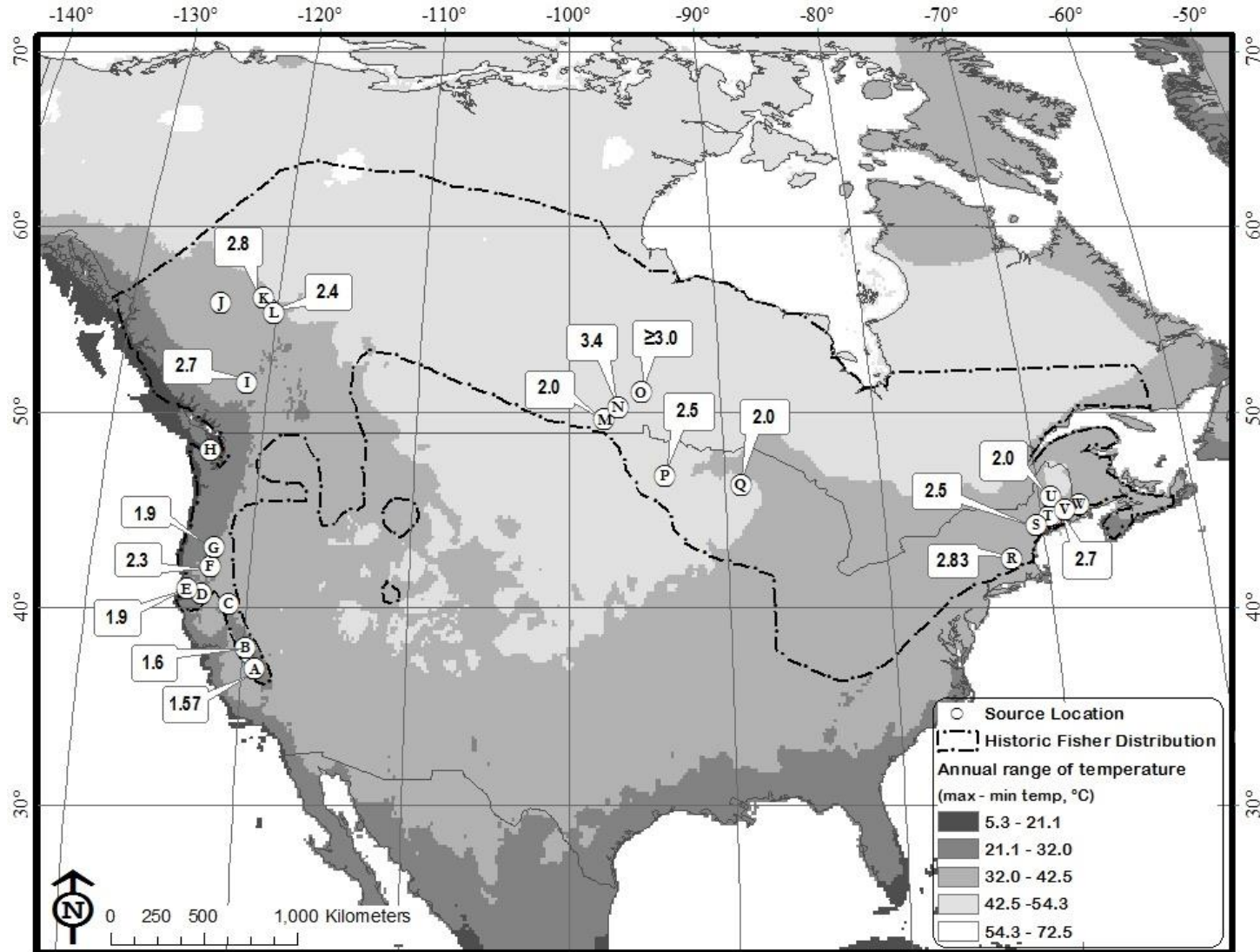


Figure 4. Mean or median (denoted by asterisks) parturition dates from 11 studies across the range of fisher in North America, including both wild (9) and captive settings (2). Study sites are arranged from north (top) to south (bottom) and letters indicate source materials referenced in Table 2. Horizontal bars represent the range of dates reported by these authors.

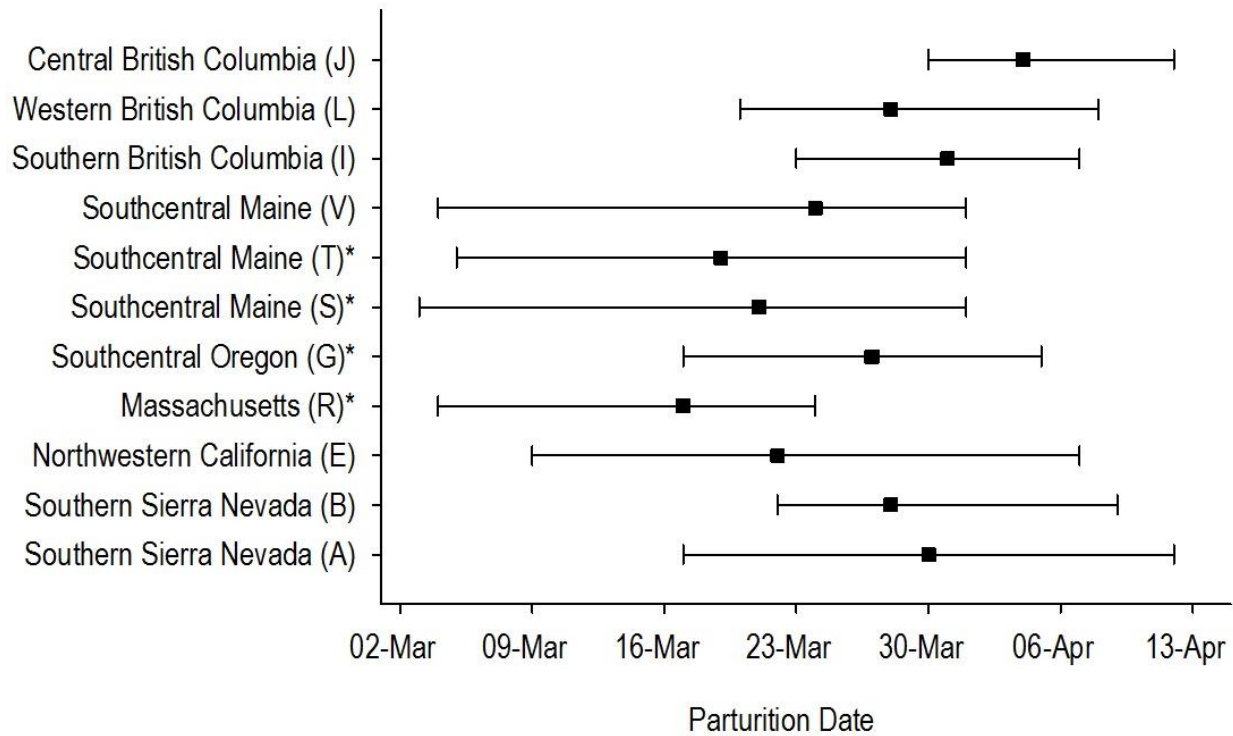


Figure 5. Results of principal components analysis showing the relationship between four bioclimatic variables and mean litter size of fisher (*Pekania pennanti*) across North America. (a) Ordination plot showing the distribution of 13 sites in bivariate space. Symbol size and symbol color reflect mean litter size (small, gray = < 2 kits/litter; medium, dark gray = 2 – 3 kits/litter; large, black = > 3 kits/litter). Vectors show the distribution of selected bioclimatic variables. Only the 1st axis is biologically interpretable, and reflects a gradient from sites with greater seasonality and variability of temperature to those with warmer mean annual temperatures and higher mean annual precipitation. (b) Regression of mean litter size on PC 1, showing a significant negative association between these parameters. Thus, sites with larger litters exhibit greater seasonality and more variable temperatures, whereas those with smaller litters are characterized by warmer sites with more precipitation.

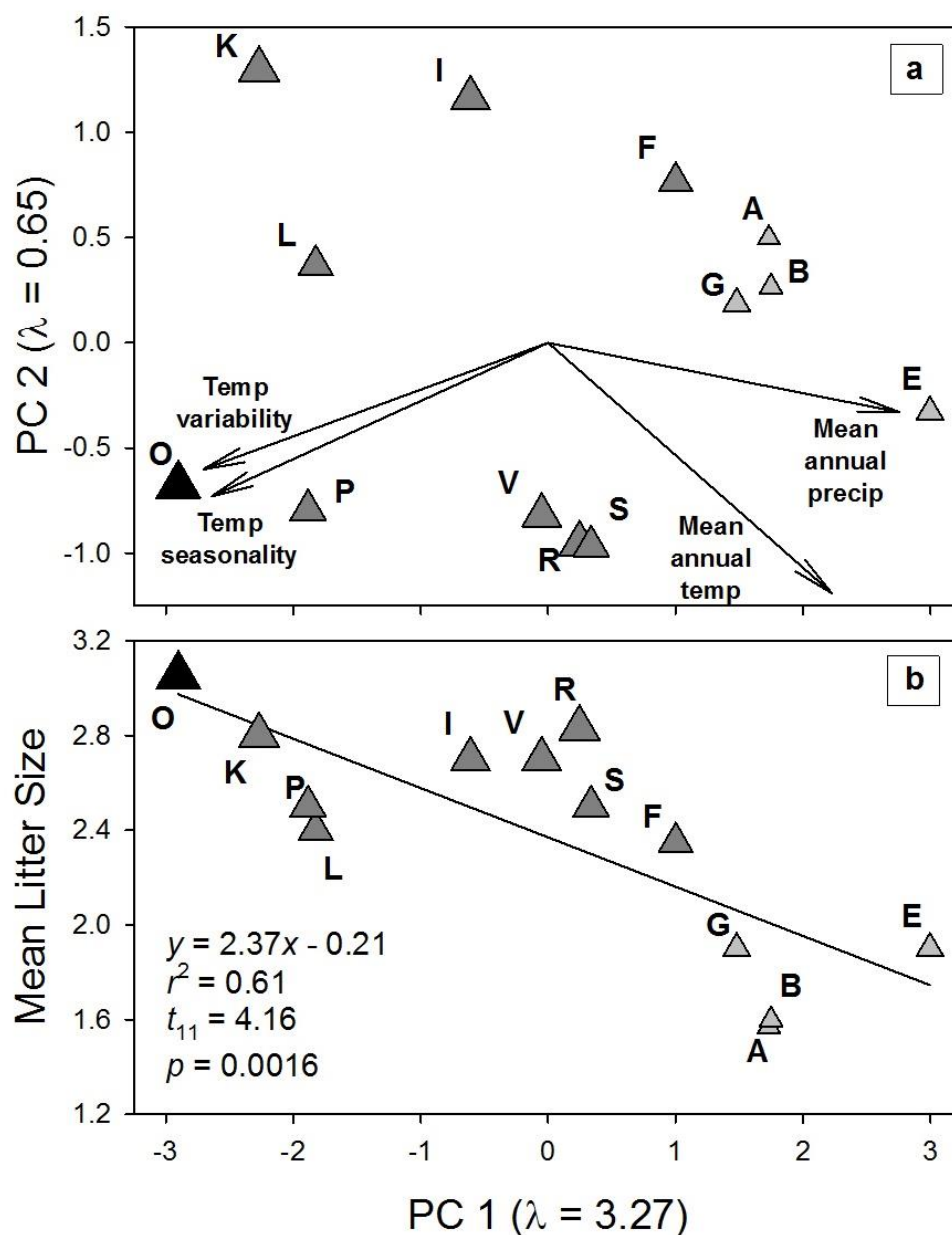


Figure 6. Timeline of dates and time periods associated with fisher reproductive activities documented on the Kings River study in the southern Sierra Nevada. Dates were confirmed using a combination of ground telemetry and remote cameras.

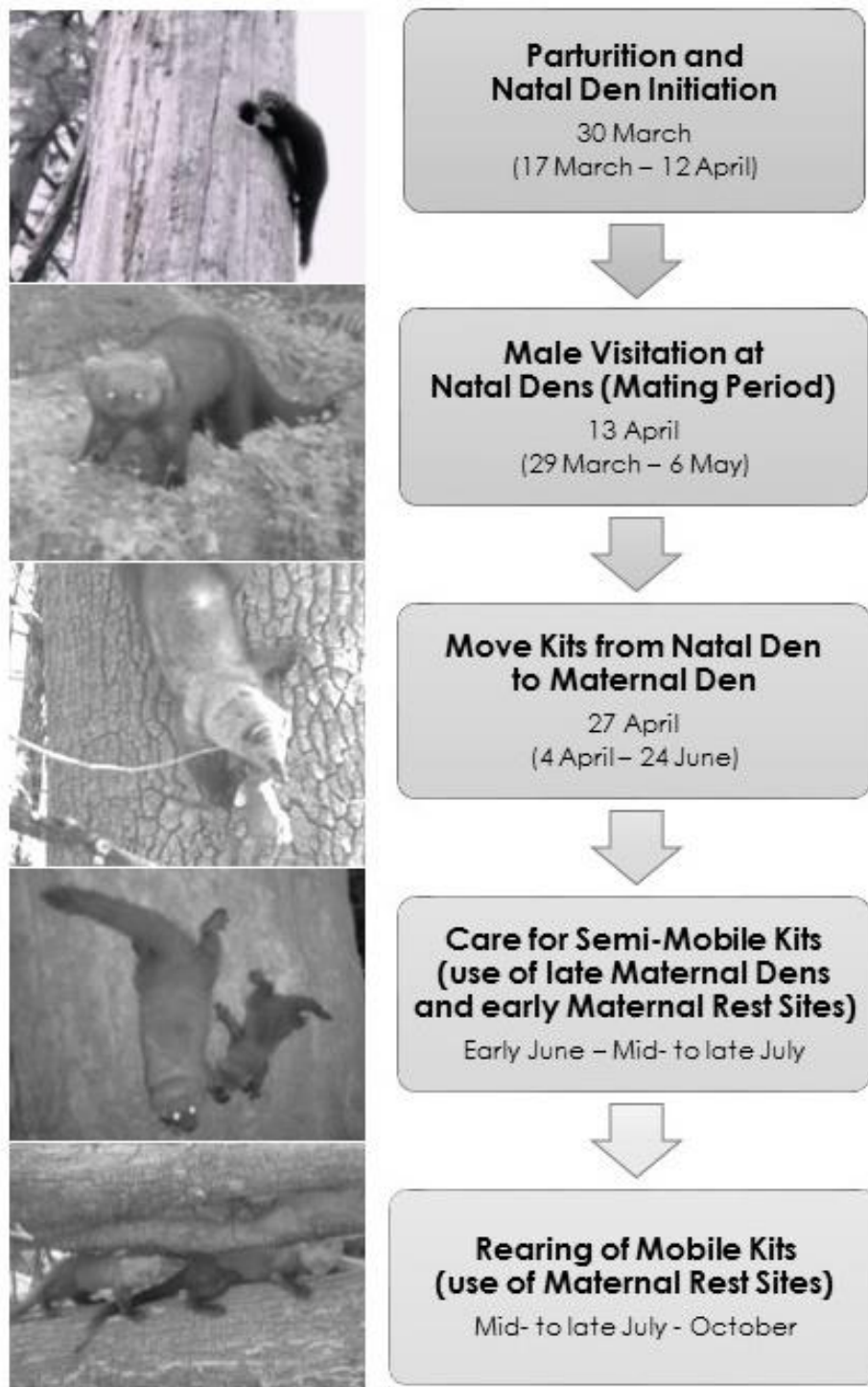
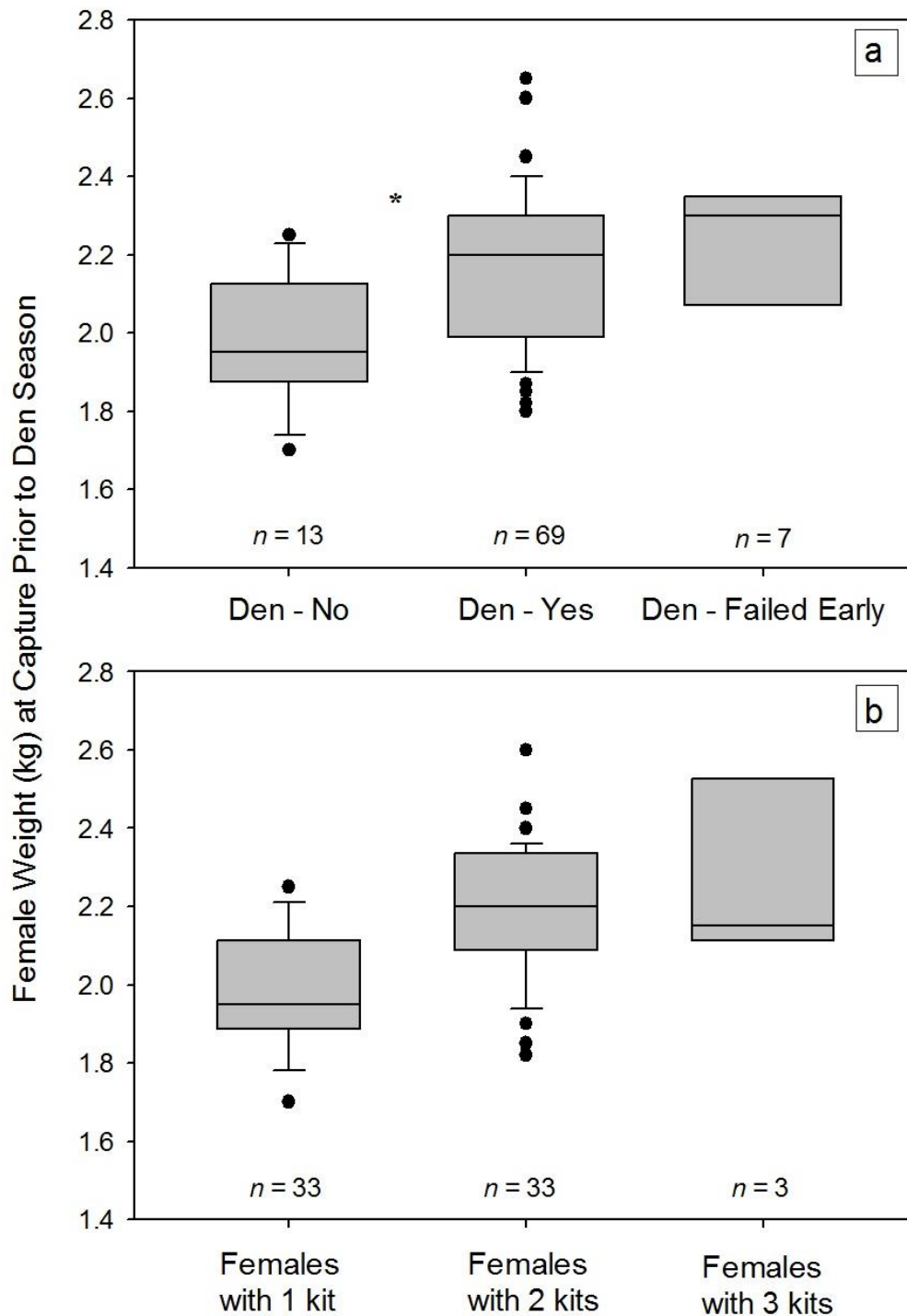


Figure 7. Weights of adult and subadult female fishers as a function of (a) denning status and (b) litter size. The top panel shows that females that failed to reproduce in the next available mating season were lighter than those females that did reproduce, and that females with failed dens were not lighter than those with successful dens. The bottom panel shows weights of females that gave birth to 1 kit compared to those who gave birth to 2 ($n = 33$) or 3 ($n = 3$) kits (b). Median weights are denoted by a line in the box plots.



Appendix A. Summary of source material related to fisher reproduction located during the literature review. Sources that contained primary data that were included in summaries within the main manuscript are highlighted in bold. Any references not included in the main manuscript are reported in Appendix C. Codes for the type of source are as follows: B (book), BC (chapter in a book), D (dissertation), FJ (fur trade journal), J (scientific journal), PC (pers. comm.), RP (report), RV (review), and T (MS thesis). Setting reflects where the animals were monitored (e.g., wild, captive (for research purposes), fur farm (captive for fur production), carcasses (generally from fur trappers)) and information on the population where relevant (e.g., animals were translocated, captured in the wild, or born in captivity).

ID	Citation	Type	Field Site	Years	Setting and Population
1	Arthur and Krohn 1991	J	Maine	1984-1987	Wild
2	Aubry and Raley 2006	RP	Oregon (S central)	1995-2002	Wild (translocated)
3	Cherepak and Connor 1992	J	Manitoba (SW)	1989-1991	Captive (wild caught, captive born)
4	Cherepak 1993	T	Manitoba	1989-1991	Captive (wild caught, captive born)
5	Clayton 2015	PC	Oregon (S central)	2013-2015	Wild
6	Coulter 1966	D	Maine	1956-1965	Captive and carcasses (wild caught)
7	Crowley et al. 1991	J	NH, VT, ME, ON	1975-1988	Carcasses (wild caught)
8	Davis 2009	T	BC (Chilcotin)	2005-2008	Wild
9	Douglas 1943	FJ	Manitoba	1940s	Fur farm (wild caught, captive born)
10	Douglas and Strickland 1987	RV	ON, North America	Carcasses 1972-1984, Prior records	Carcasses (wild caught)
11	Eadie and Hamilton 1958	J	New York	1950s	Carcasses (wild caught)
12	Enders and Pearson 1943	J	Unclear	1943	Unclear
13	Erb et al. 2014	RP	Minnesota	2008-2014	Wild
14	Facka et al. 2016	J	California, Washington	2008-2012	Wild (translocated)
15	Frost and Krohn 1997	BC	Maine	1990-1993	Captive (wild caught)
16	Frost and Krohn 2004	BC	Maine	1991-1993	Captive (wild caught)
17	Frost et al. 1997	J	Maine	1991-1993	Captive (wild caught, captive born)
18	Frost et al. 1999	J	Maine	1990-1993	Captive (wild caught, captive born)
19	Frost et al. 2005	J	Maine	1991-1992	Captive
20	Green et al., this study	J, D	California (Sierra)	2007-2014	Wild
21	Grinnell et al. 1937	BC	California	Prior records	Wild
22	Hall 1942	J	BC, California	Fur farm 1933-1938, Traps 1925-1940	Fur farm (wild caught, captive born)

23	Hamilton and Cook 1955	J	New York	1950-1953	Carcasses (wild caught)
24	Hodgson 1937	B	Canada (N Ontario)	Prior records	Fur farm (wild caught, captive born)
25	James et al. 2008	R	California (northwest)	2006-2007	Wild
26	Kelly 1977	D	New Hampshire	1973-1975	Wild and carcasses (wild caught)
27	Laberee 1941	FJ	Canada (Ottawa)	Prior records	Fur farm (wild caught, captive born)
28	Leonard 1986	J	Manitoba	1972-1978	Wild, captive, carcasses (wild caught)
29	Lofroth et al. 2010	RV	North America (west)	Prior studies/records	All
30	Matthews et al. 2013a	J	California (northwest)	2005-2011	Wild
31	Matthews et al. 2013b	J	California	2004-2011	Wild
32	Mead 1994	RV	North America	Prior studies/records	All
33	Paragi 1990	T	Maine	1984-1989	Wild and carcasses (wild caught)
34	Paragi et al. 1994	J	Maine	1988-1989	Wild
35	Paragi et al. 1996	J	Maine	1984-1989	Wild
36	Powell 1977	D	Michigan (north)	1973-1976	Captive (wild caught)
37	Powell 1981	RV	North America	Prior studies/records	All
38	Powell 1993	B	North America	Prior studies/records	All
39	Powell and Leonard 1983	J	Manitoba	1977	Wild
40	Powell et al. 1997	BC	Mass., New Hampshire	1992-1995	Wild
41	Powell et al. 2003	RV	North America	Prior studies/records	All
42	Self and Callus 2006	RP	California (northwest)	2006	Wild
43	Shea et al. 1985	J	Maine	1978-1981	Wild
44	Simpson et al. 2013	RP	BC (Peace Region)	2011-2012	Wild
45	Sweitzer et al. 2015	J	California (Sierra)	2007-2013	Wild
46	Truex et al. 1998	RP	California	1992-1998	Wild
47	Weckworth and Wright 1968	J	Montana (west)	1959-1966	Wild (translocated)
48	Weir 2009	RP	BC (Dawson Creek)	2008-2009	Wild
49	Weir and Corbould 2008	RP	BC (Williston)	1996-2000	Wild
50	Weir et al. 2012	J	BC (Dawson Creek)	2005-2009	Wild
51	Weir unpub. data 2014	PC	BC (Dawson Creek)	2005-2009	Wild
52	Wright and Coulter 1967	J	Maine	1950-1964	Wild
53	York 1996	T	Massachusetts	1992-1995	Wild
54	Zhao et al. 2012	J	California	2007-2011	Wild

Appendix B. Summary of source information related to fisher reproduction located during the literature review. Sources containing primary data that were included in summaries in the main manuscript are highlighted in bold. Under methods, options included: Dens (reproductive dens were located), Telemetry (telemetry was used in monitoring animals), Captive (animals were observed in captivity), Repro. Tracts (reproductive tracts were examined), and Teats (teats were assessed or measured to indicate whether lactation or reproduction occurred). Under reproductive parameter data, options included: % Repro. (percent or proportion of females that reproduced), P Date (date of parturition), Litter size (RT) – (data related to litter size was determined from reproductive tracts, including counts of corpora lutea, blastocysts, placental scars, embryos, or fetuses), Litter size (Kits) – (data on litter size came from kit counts after parturition), and Mating (data on timing or behaviors associated with mating).

ID	Citation	Methods	Reproductive Parameter Data Available
1	Arthur and Krohn 1991	Dens, Telemetry, Teats	% Repro, P Date
2	Aubry and Raley 2006	Dens, Telemetry, Teats	% Repro, P Date, Litter size (Kits)
3	Cherepak and Connor 1992	Captive	P Date
4	Cherepak 1993	Captive	% Repro, Mating
5	Clayton 2015	Dens, Telemetry	% Repro, P Date, Litter size (Kits)
6	Coulter 1966	Captive, Repro. Tracts	P Date, Litter size (RT, Kits)
7	Crowley et al. 1991	Repro. Tracts	% Repro, Litter size (RT)
8	Davis 2009	Dens, Telemetry	
9	Douglas 1943	Captive	P Date, Litter size (Kits)
10	Douglas and Strickland 1987	Repro. Tracts	% Repro, P Date, Litter size (RT, Kits)
11	Eadie and Hamilton 1958	Repro. Tracts	Litter size (RT)
12	Enders and Pearson 1943	Repro. Tracts	Litter size (RT)
13	Erb et al. 2014	Dens, Telemetry, Repro. Tracts	% Repro, P Date, Litter size (Kits)
14	Facka et al. 2016	Dens, Telemetry	% Repro
15	Frost and Krohn 1997	Captive	% Repro, P Date, Litter size (Kits)
16	Frost and Krohn 2004	Captive	% Repro, P Date, Litter size (Kits)
17	Frost et al. 1997	Captive	% Repro, P Date
18	Frost et al. 1999	Captive, Repro. Tracts	
19	Frost et al. 2005	Captive	% Repro, P Date, Litter size (Kits)
20	Green et al., this study	Dens, Telemetry, Teats	% Repro, P Date, Litter size (RT, Kits), Mating
21	Grinnell et al. 1937	(Observation)	Litter size (Kits)
22	Hall 1942	Captive	P Date, Litter size (Kits), Mating

23	Hamilton and Cook 1955	Repro. Tracts	P Date, Litter size (RT, Kits)
24	Hodgson 1937	Captive	P Date, Litter size (Kits), Mating
25	James et al. 2008	Dens, Telemetry	% Repro
26	Kelly 1977	Dens, Telemetry, Repro. Tracts, Teats	Litter size (RT)
27	Laberee 1941	Captive	Mating
28	Leonard 1986	Dens, Telemetry, Captive, Repro. Tracts	% Repro, P Date, Litter size (RT, Kits)
29	Lofroth et al. 2010	Summary	% Repro, P Date, Litter size (RT, Kits), Mating
30	Matthews et al. 2013a	Dens, Telemetry	% Repro, P Date, Litter size (Kits)
31	Matthews et al. 2013b	Dens, Teats	
32	Mead 1994	(Summary)	P Date, Litter size (Kits), Mating
33	Paragi 1990	Dens, Telemetry, Repro. Tracts, Teats	% Repro, P Date, Litter size (RT, Kits)
34	Paragi et al. 1994	Dens, Telemetry	% Repro, Litter size (Kits)
35	Paragi et al. 1996	Dens, Telemetry	P Date
36	Powell 1977	Captive	% Repro, P Date, Litter size (Kits)
37	Powell 1981	(Summary)	% Repro, P Date, Litter size (Kits), Mating
38	Powell 1993	Captive	% Repro, P Date, Litter size (RT, Kits), Mating
39	Powell and Leonard 1983	Dens, Telemetry, Repro. Tracts	% Repro, P Date, Litter size (RT, Kits)
40	Powell et al. 1997	Dens, Telemetry	P Date
41	Powell et al. 2003	(Summary)	P Date, Litter size (RT, Kits), Mating
42	Self and Callus 2006	Dens, Telemetry	% Repro, P Date
43	Shea et al. 1985	Repro. Tracts	% Repro, Litter size (RT)
44	Simpson et al. 2013	Dens, Telemetry	P Date, Litter size (Kits)
45	Sweitzer et al. 2015	Dens, Telemetry, Teats	% Repro, P Date, Litter size (Kits)
46	Truex et al. 1998	Dens, Telemetry, Teats	% Repro, P Date
47	Weckworth and Wright 1968	Repro. Tracts	P Date, Litter size (RT), Mating
48	Weir 2009	Dens, Telemetry	% Repro, P Date, Litter size (Kits)
49	Weir and Corbould 2008	Dens, Telemetry	% Repro, P Date
50	Weir et al. 2012	Dens, Telemetry	
51	Weir unpub. data 2014	Dens, Telemetry	% Repro, P Date, Litter size (Kits)
52	Wright and Coulter 1967	Repro. Tracts	P Date, Litter size (RT), Mating
53	York 1996	Dens, Telemetry	% Repro, P Date, Litter size (Kits)
54	Zhao et al. 2012	Dens, Telemetry	

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CHAPTER 2

Habitat associated with fisher (*Pekania pennanti*) reproduction in the southern Sierra Nevada: a comparison of forest features used for denning relative to resting and evaluation of habitat selection at reproductive dens

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ABSTRACT Many species of wildlife rely on unique features of trees during daily activities and fundamental parts of their life cycle; some elements of the greatest value to forest-dwelling wildlife take long periods of time and multiple ecological processes to develop. The fisher (*Pekania pennanti*) is an arboreal carnivore of conservation concern in western North America that uses forest structures with specific features (e.g., tree cavities) as refuges during reproduction and daily resting bouts; prior to this study, little was known about the habitat associated with reproduction at the southernmost extent of the fisher's range which is warmer

and more xeric than boreal parts of this species' range. We document fisher use of microsites and structures for resting and reproduction in the southern Sierra Nevada, and characterize habitat selection by reproductive female fishers at 3 spatial scales – structure, site, and stand. Between 2007 and 2015, we attached radio-collars to 55 male and 72 female fishers. We documented resting locations of males on 216 occasions (196 structures) and females on 824 occasions (737 structures). Beginning in 2008, we monitored female fishers over 8 reproductive seasons and confirmed 45 females at dens during ≥ 1 reproductive season; we located 95 natal dens (83 structures) and 206 maternal dens (192 structures). At the microsite scale, male and female fishers rested in tree cavities (42.1%), branch platforms (29.7%), broken top platforms (11.1%), burrows (8.4%), and log cavities (7.5%); in contrast, reproductive females used tree cavities almost exclusively as natal (100.0%) and maternal den (99.0%) microsites. At the structure scale, male and female fishers rested in live conifers (35.4%), live hardwoods (26.3%), and conifer snags (20.1%) most often, while denning females used live hardwoods (51.3%), live conifers (22.5%), and conifer snags (21.3%). Both sexes used white fir (*Abies concolor*), California black oak (*Quercus kelloggii*), and ponderosa pine (*Pinus ponderosa*) as rest structures most often; for den structures, females used California black oaks most frequently (55.4%), followed by white fir and incense cedar (*Calocedrus decurrens*). Habitat selection analysis suggested that large California black oaks, large snags, dense canopy cover, high stand density index values, and evidence of decay combined with greater slope and lower elevation predict fisher den habitat at different spatial scales. Conservation of forest suitable for fisher reproduction in the southern Sierra Nevada would benefit from increased focus on retaining large structures, especially California black oak, with long-term plans to replace old decadent trees.

Key words: den, fisher, *Pekania pennanti*, reproduction, rest, Sierra Nevada

1. Introduction

Forests provide resources for wildlife species at multiple temporal and spatial scales (Bissonette et al. 1997, George and Zack 2001). Many forest resources, such as seeds, fruits, and deciduous leaves, vary in availability during the year in accordance with the life cycles of individual plant species; forest resources also vary seasonally in their value to wildlife, with the most critical resource needs often tied to periods of highest energetic costs during reproduction and raising of young (Blakesley et al. 2005, van der Heide et al. 2011, Nemes and Islam 2016). Forest-dwelling wildlife make use of a wide spatial spectrum of features including fine-scale elements (e.g., tree cavities, bark crevices), structural attributes (e.g., tree diameter and height), characteristics created by clusters of trees (e.g., canopy cover), and qualities of broad-scale areas of forest (e.g., percentage of hardwood trees; Lacki and Schwierjohann 2001, Ramos-Lara et al. 2013, Amelon et al. 2014, Deng and Zhang 2016). Hence, habitat selection may be affected by multiple forest resources, although habitat elements that are essential or rare can have a disproportionate influence on selection compared to resources that are commonly available or less critical to survival (Webb et al. 2012, Edworthy 2016, Wilk et al. 2016). Habitat conservation efforts for forest-dwelling species of concern can be advanced by characterizing suitable habitat at appropriate spatial scales, identifying resources that support essential activities (e.g., reproduction), and ascertaining temporal variation in availability or use of key resources (Gorman et al. 2006, Zimmerman and Gutiérrez 2008, Gruebler et al. 2014, Cockle et al. 2015).

Not all contemporary forests are equal in their capacity to sustain wildlife species year-round and support fundamental seasonal activities such as reproduction. Some features of value to wildlife take many years to develop and thus are more likely to be found in mature and old-growth forests than young or regenerating forests (Mazurek and Zielinski 2004, Cockle et al.

2010, Weir et al. 2012). Older forests are commonly characterized by dense canopy cover, large diameter trees, and a sustained supply of forest elements (e.g., large snags and logs; Oliver and Larson 1996). Less commonly recognized are the contributions made by individual older trees with unique decadent features such as cavities, basal hollows, and deep bark crevices which are used as refuges by wildlife during rest and reproductive activities (Ryan and Vaughn 2004, Gess et al. 2013, Ramos-Lara et al. 2013, de la Parra-Martínez et al. 2015, Otto et al. 2016). Many of the unique characteristics of trees of high value to wildlife require time to develop, but tree species distribution, biotic factors, abiotic conditions, and local land management history can also influence forest structure and availability of specific elements (Hale et al. 1999, Siitonen et al. 2000, Munteanu et al. 2016). Loss and alteration of mature forest habitats have led, at least in part, to conservation concern for a growing number of wildlife species in temperate and tropical forests (Angelstam and Mikusiński 1994, Sodhi et al. 2004, Buehler et al. 2008, Virkkala 2016). Increased awareness of the complex ecological relationships operating in mature forests can help identify the habitat needs of forest specialists and facilitate the development of habitat conservation plans that can help species of concern persist in the short- and longer-term (Buskirk and Zielinski 2003, Wesółowski 2011, Weir et al. 2012, Zahner et al. 2012).

The fisher (*Pekania pennanti*) is a North American mustelid carnivore that is ecologically tied to mature forest (Purcell et al. 2009, Weir et al. 2012). Since European settlement, the range of the fisher has been reduced by approximately 50% (Laliberte and Ripple 2004), with declines occurring largely in areas where extensive fur trapping has overlapped with timber harvest (Lofroth et al. 2010). Fishers favor older forests containing large diameter trees, dense canopy cover, and decadent features (Carroll et al. 1999, Zielinski et al. 2004a, Purcell et al. 2009, Gess et al. 2013). Fishers use numerous sites for daily resting bouts, possibly corresponding to their

relatively large home ranges (Zielinski et al. 2004a, 2004b). In spring, however, the movements of reproductive female fishers become more centralized once they give birth and begin caring for their young in tree cavities (Paragi et al. 1996, Powell et al. 2003, Weir et al. 2012). Parturition occurs in a natal den and females may move their kits to 1 or more maternal dens through early summer (Green et al. 2017a). Individual females may use up to 6 structures in a single den season (Matthews et al. 2013). The moderately large body size of fishers suggests that trees with cavities that can accommodate a female and her kits may be uncommon even in pristine landscapes; in managed forests, availability of suitable trees for denning may be limited. Due to these life-history traits and the current status of forests in the Pacific Northwest and the southern Sierra Nevada, fishers are currently of conservation concern (Lofroth et al. 2010); populations in the southernmost portion of the range may be especially vulnerable due to low population size (Spencer et al. 2011), isolation from northerly populations (Zielinski et al. 2005), low genetic diversity (Wisely et al. 2004), elevated risk of stand-replacing fires (Miller et al. 2009), predation by larger carnivores (Wengert et al. 2014), exposure to rodenticides (Gabriel et al. 2012), and more broadly, climate change (Parmesan and Yohe 2003, Parmesan 2006, Lawler et al. 2012).

The types of structures and habitat used by fishers for resting are relatively well known (Zielinski et al. 2004a, Purcell et al. 2009, Gess et al. 2013), but research focused on the habitat needs of females during reproduction is still quite limited (Paragi et al. 1996, Powell et al. 1997, Weir et al. 2012). Relative to resting habitat, females are likely to use more specialized criteria when selecting habitat, and specific sites, to raise young (Fig. 1). Prior to 2008, only a handful of reproductive dens (defined in Table 1) had been documented in the Sierra Nevada; consequently, data to help identify, and thus conserve, suitable reproductive habitat in the southernmost portion of the fisher's range were virtually unavailable. Grinnell et al. (1937)

reported observations from 1912 of a female fisher and 3 older kits seen emerging from a protected space under a granite slab in a forested area on several occasions during late June and early July. Truex et al. (1998) located 5 spring reproductive dens and 3 structures in which older mobile kits were seen with adult females in the summer; the dominant tree species used in these instances were California black oak (*Quercus kelloggii*) and white fir (*Abies concolor*). These reports summarize what was previously documented about reproductive habitat of fisher in the Sierra Nevada. While descriptions of habitat use associated with reproduction from other areas (e.g., boreal forest of Canada and the northern Midwest) are informative, forest management history and the distribution of tree species vary widely across the fisher's range; evaluation of habitat requirements for female fishers during reproduction obtained in the southern Sierra Nevada could better inform conservation plans for this region.

Conservation plans to manage forests for fishers and species dependent on similar forest attributes (e.g., goshawk, *Accipiter gentilis*; spotted owl, *Strix occidentalis*) require an understanding of habitat use and selection by reproductive females (Lileiholm et al. 1994, Blakesley et al. 2005). To this end, we pursued a relatively long-term study of the habitat used for denning by reproductive female fishers in the southern Sierra Nevada, employing 2 complimentary approaches. To assess habitat use, we quantified fine-scale habitat features (microsites, structures) used by all fishers (sexes combined) for general resting needs relative to features used only by denning females. For this we compared characteristics of microsites and structures used by (a) resting male versus resting female fishers, (b) denning female fishers at natal versus maternal dens, and (c) resting fishers (male and female locations combined) versus denning female fishers (natal and maternal dens combined). We also evaluated habitat selection

for reproductive females by comparing habitat at known den locations (natal and maternal) with available habitat at random sites across 3 spatial scales (structure, site, stand).

We developed 8 hypotheses associated with our objectives based on fundamental aspects of fisher ecology and on previous studies of habitat use. Male fishers are generally larger than females (Powell et al. 2003), so may be less vulnerable to predation and cold temperatures while resting; as such, (H1) we expected females to be more restricted in their use of microsites and structures relative to males. Because female fishers favor large-diameter hardwood trees with cavities as reproductive dens (Paragi et al. 1996, Weir et al. 2012), (H2) we expected females to select tree cavities more often than other microsite types and (H3) to disproportionately favor hardwood species and trees of large diameter when denning compared to resting. We expected the habitat characteristics of natal and maternal dens to be broadly similar; however, we hypothesized that (H4) natal den microsites would be higher than maternal dens to potentially increase safety and solar exposure, and (H5) canopy cover would be lower around natal dens to allow for greater solar exposure on microsites containing young kits. In comparing den structures to available structures within the same forest stand, (H6) we expected female fishers to select trees of hardwood species, with larger diameters and more decay compared to available trees based on studies of reproductive dens in other geographic areas (Paragi et al. 1996, Weir et al. 2012). We also anticipated that females would (H7) select sites with greater canopy and understory cover compared to available sites due to known close associations of fishers with dense canopy cover at rest locations (Zielinski et al. 2004a) and hypothesized use of understory cover as visual concealment to reduce risk of predation (Wengart et al. 2014). Finally, based in part on previous work in the Sierra Nevada (Zielinski et al. 2004b, Purcell et al. 2009), (H8) we hypothesized that forest stands containing reproductive dens would be characterized by greater

availability of large snags and hardwoods, higher basal area, and denser canopy cover than randomly selected stands.

2. Material and methods

2.1.1 Study area

Our research was conducted between June 2007 and December 2015 in the Sierra National Forest southeast of Shaver Lake, California, USA (37° 3' N, 119° 11' W). The study area encompassed roughly 43,500 ha of forested land on the western slopes of the southern Sierra Nevada (Fig. 2). We focused live trapping efforts at elevations from 1,000 to 2,000 m; although most individual animals remained within this elevation zone after release, some traveled above or below this range. Precipitation generally occurs in fall (rain) and winter (snow at elevations $\geq 1,500$ m); during the final 2 years of the study, precipitation levels were well below normal levels for the southern Sierra Nevada (Mann and Gleick 2015).

Within the study area, forested habitats were dominated by conifer species at higher elevations and a mixture of hardwood and conifer species at lower elevations. Hardwood tree species (in descending order of relative abundance) included California black oak, Canyon live oak (*Q. chrysolepis*), white alder (*Alnus rhombifolia*), and big leaf maple (*Acer macrophyllum*). Coniferous tree species in the area included (most to least abundant) white fir, incense cedar (*Calocedrus decurrens*), ponderosa pine (*P. ponderosa*), sugar pine (*P. lambertiana*), and Jeffrey pine (*Pinus jeffreyi*). Vegetation types within the study area included montane hardwood forest, montane hardwood-conifer forest, ponderosa pine forest, Sierran mixed-conifer forest, white fir forest, and montane chaparral, as described by the California Wildlife Habitat Relationship classification (Mayer and Laudenslayer 1988; www.wildlife.ca.gov/Data/CWHR/Wildlife-Habitats); meadows and areas of open granite were also scattered throughout this primarily

forested landscape. Most of the land within the study area is managed by the United States Forest Service (USFS), but portions are owned by Southern California Edison and other private land owners. Over the last century, management activities on this landscape included timber harvest, prescribed fire, and urban development, although areas of mature forest and patches of large remnant trees were retained. Fire suppression has also led to increases in shade-tolerant species (e.g., white fir, incense cedar) and fuels (Fites-Kaufman et al. 2007).

2.2 Animal handling

We concentrated live-trapping efforts for fishers in the autumn and winter (October through February); trapping during this period reduced chances of catching females that were either close to parturition or nursing young kits in spring, avoided capture of juveniles that were too small for radio-collar attachment, and minimized interference from black bears (*Ursus americanus*) in summer. We caught fishers in box traps (32 x 10 x 12 in, original series model 108, Tomahawk Live Trap, Hazelhurst, WI) with a wooden box (cubby) affixed at the back; the cubby served as a refuge to reduce stress and self-inflicted injuries (e.g., broken canines). We covered traps with bark and other natural materials to provide camouflage and insulation. During cold periods, we placed a piece of fleece material (roughly 30 cm x 50 cm) inside the cubby for insulation, and stiff corrugated black plastic (Coroplast, Vanceburg, KY) over the trap to keep the interior dry. We baited traps with chicken placed inside a sock and tied to the top of the trap behind the treadle; we smeared a bait lure on the sock inside the trap (Hawbaker's Fisher Lure, Hawbaker and Sons, Fort Loudon, PA or Fisher Red Lure, Proline Lures, Indianapolis, IN), and applied a call lure on a nearby tree outside the trap (Caven's Gusto, Minnesota Trapline Products, Pennock, MN or Outreach Call Lure, Proline Lures, Indianapolis, IN). Bait was

replaced as needed if absent, partially eaten, or desiccated (≤ 7 day intervals); bait lure was refreshed when chicken was replaced and call lure was refreshed every 3 days.

We checked all traps every morning; fishers that either did not have radio-collars or needed a replacement collar were processed at the site of capture once all traps were checked. To facilitate radio-collar attachment, fishers were coaxed out of the trap cubby, through a thick canvas sleeve, and into a heavy metal handling cone (Seglund 1995). We estimated sex and weight of animals, then sedated them with an intramuscular injection of Ketamine (22.5 mg/kg) mixed with Diazepam or Midazolam (0.125 mg/kg). Once docile, animals were removed from the handling cone and weighed. We applied eye ointment, affixed an eye cover, checked their airway, and monitored temperature and respiration; we maintained body temperature within a safe range (100 – 102°F) while anesthetized by applying heat packs or rubbing alcohol as needed; drugs were administered conservatively, and supplemental injections were given if needed.

Fishers ≥ 1.7 kg were fitted with Holohil radio-collars (model MI-2M, 31 grams, Holohil Systems Ltd., Carp, Ontario, Canada) equipped with a handmade breakaway device; we attached Advanced Telemetry Solutions (ATS) collars (model 1920, 38 grams, ATS, Inc., Isanti, MN) to a few individuals in 2007, and we fitted a subset of males (subadults and adults ≥ 3.0 kg) with GPS collars with a VHF component (Quantum 4000E micro mini GPS, 65-80 grams, Telemetry Solutions, Concord, CA). Holohil collars weighed $< 2\%$ of body weight while ATS and GPS collars were $< 3\%$; in this report, we only use data obtained using VHF signals (i.e., data downloaded from GPS collars were not used here). Morphological measurements were taken and animals were marked with Passive Integrated Transponder (Biomark, Boise, ID) tags. Age class (adult, subadult, juvenile) was determined based on a combination of molar wear,

development of sagittal crest, and teat condition in females as outlined in Green et al. (2017a). Once anesthesia began to wear off (typically 40 min after injection), fishers were returned to the cubby, where they were held until fully recovered and then released (generally 60 min after placement back in cubby). Capture and handling procedures have been described in further detail in Green et al. (2017a) and were approved by the Institutional Animal Care and Use Committee of the University of California, Davis.

2.3 Location of Fisher Rest Sites and Reproductive Dens

During daily monitoring efforts, we opportunistically located inactive radio-collared fishers using a combination of triangulation and homing techniques to identify structures used for resting (see Zielinski et al. (2004a) and Purcell et al. (2009) for details on these techniques). To distinguish unique habitat components at different spatial scales, we adopted terms and descriptions used previously (Slauson and Zielinski 2009, Matthews et al. 2013) with modifications and additions based on our field experience (Table 1).

From early March through June we focused telemetry efforts on inactive adult females in early morning hours to locate reproductive dens, following field protocols used previously in California (Matthews et al. 2013). When locating both rest and den structures, we typically used triangulation to reach the vicinity of individual animals, and after confirming an inactive signal for ≥ 20 minutes we used homing techniques to locate the rest or den structure. When approaching an inactive fisher, we proceeded towards the triangulated location but monitored the transmitter signal to maintain correct direction and detect fluctuations indicating the animal had become active. Once near the inactive fisher, we circled the area as quietly as possible until we narrowed the signal down to 1 structure; if we could not narrow the signal to a single structure or if the animal left before the structure was identified, we documented the location as a rest area,

but excluded those locations from analyses. Using these methods, we were confident that we located all (or nearly all) reproductive den structures used each year by radio-collared female fishers due to concentrated efforts; in contrast, we located a subset of the total number of rest structures used by male and female fishers throughout the year, although these locations were relatively well distributed across individual animals, seasons, and years.

If an individual rest or potential den structure was identified, we attempted to locate the microsite using visual clues and the transmitter signal. In many cases, we were able to identify a single feature as the only apparent microsite (e.g., cavity in log) consistent with the transmitter signal, and occasionally we observed the fisher (Appendix A). Den microsites sometimes showed evidence of repeated use (e.g., hairs at cavity entrance visible with binoculars); a subset of microsites were also verified during efforts to count offspring using additional techniques (e.g., tree climb, remote camera; Green et al. 2017*a, b*). If we could not identify a specific microsite with confidence, we recorded it as unknown.

2.4 Vegetation Measurements

During initial location of a radio-collared fisher at a rest or reproductive den structure, we recorded the coordinates using a hand-held GPS unit, marked the site with flagging, noted the location of the microsite (if identified), and described the structure (e.g., tree species, estimated tree diameter). To minimize disturbance, we sketched a diagram of key features and returned at a later date when the site was not occupied to measure features of the microsite, structure, surrounding cover, or stand. Because deciduous trees and shrubs are distributed throughout the study area we measured canopy cover, understory cover, and stand level characteristics at reproductive dens only during summer and early fall to ensure comparable data across sites.

2.4.1 Microsites and structures used for resting and denning – fisher habitat use

To describe *fisher habitat use* we recorded measurements of microsites and structures at a large subset of rest locations (male and female) and at all reproductive dens (natal and maternal) when these structures were not in use. If a microsite was identified at a structure, we assigned a microsite type (e.g., tree cavity), measured microsite height using a hypsometer or tape measure, and described the known or suspected entrance (e.g., woodpecker hole, broken limb). In the case of cavities and burrows, we considered microsite height to be the distance from the ground to the entrance, although the actual location of the resting fisher may have been below ground level; as we generally did not observe the fishers in these ground level locations (e.g., burrow, log, slash pile), heights were often estimated to be between 0 – 0.5 m depending on the characteristics of the structure. We categorized structures used for resting or denning by type (e.g., live hardwood, conifer snag), measured aspect with a compass, and determined slope (%) with a clinometer. For structures identified as live trees, snags, or logs, we identified tree species, determined tree/snag height using a hypsometer, and measured diameter at breast height (dbh) and log length. We recorded decay class for standing trees according to Maser et al. (1979), where a value of 1 represents a live healthy tree, 2 denotes a live declining tree, and 3 through 9 indicate dead trees with increasing levels of decay.

2.4.2 Comparison of dens and available habitat at 3 spatial scales – fisher habitat selection

To assess *fisher habitat selection*, we compared characteristics of habitat used for reproduction with available habitat at 3 spatial scales: structure, site, and (forest) stand (Table 1). At the structure scale, we characterized habitat at reproductive dens found between 2008 and 2012, and at paired random trees within the stand containing these dens (Fig. 3a). To standardize the selection of random trees, we used the layout for a cluster of 5 Common Stand Exam (CSE) plots which were established independently to collect stand level data; details of the CSE plots

are described below (Fig. 3b) and in USFS (2013). We randomly selected 1 of the outer CSE plots; there, we selected the nearest live tree or snag within the outer (distal) half of the circle which met a priori criteria for diameter and decay. For diameter, random trees had a dbh ≥ 42 cm (hardwoods) or ≥ 76 cm (conifers); these values were based on previously documented fisher rest sites in California (Zielinski et al. 2004a). Decay criteria (not equivalent to the decay classes of Maser et al. 1979) were employed as proxies for the probability of cavities, since not all tree cavities can be observed (Cockle et al. 2010); additionally, visible openings do not always lead to cavities with dry interiors or suitable dimensions for female fishers (R. Green, personal observation). Signs of decay used as proxies for the potential presence of a cavity in the selection of random trees included one or more of the following: observation of a cavity (any size) in the tree bole, cavity (any size) in a branch, basal hollow, broken top, dead top, large (≥ 12 cm dia.) dead limb, large (≥ 12 cm dia.) broken limb, insect infestation in the tree bole (e.g., termites), mistletoe, fungus/conks, woodpecker activity, or signs of sapsucker foraging. If no random trees met both criteria, we selected a new random outer CSE plot until an appropriate tree was found. At dens and paired random trees we measured the same characteristics as with rest and den structures (e.g., tree species, dbh, height, decay level, slope, aspect), plus the presence of decay-related features.

At the site scale, we recorded measurements at the same den and random trees used above for the structure scale. We measured both canopy and understory cover to quantify concealment around the structure (Fig. 3a). Canopy cover was measured around den and random trees along linear transects in each cardinal direction; north and south transects included 4 proximal and 3 distal sampling points each, whereas east and west transects included 3 proximal and 3 distal points each (hence, a total of 14 proximal and 12 distal points; Fig. 3a). At each

point along the transect we recorded tree canopy using a moosehorn device (Moosehorn CoverScopes, Central Point, OR). The moosehorn allows estimation of canopy cover by use of a mirror arranged at a 45° angle and marked with a 5x5 grid; cover is estimated by tallying the number of grid intersections (of 25 possible) covered by canopy. For each site (den and random tree) we characterized proximal cover as the mean of all 14 proximal points. At den trees (but not random trees) we also recorded moosehorn canopy measurements at the 12 distal points along these transects for comparison with the proximal 14 points, allowing us to compare the cover at the den site with that of adjacent forest (Fig. 3a).

Horizontal understory cover was measured using a cover cloth (3 m tall x 0.5 m wide and covered with 10 cm x 10 cm grid cells; Noon 1981) attached to a pole and held by a field assistant at a distance of 10 m from the den or random tree in each cardinal direction (Fig. 3a). An observer at the center of the plot recorded the number of grid cells $\geq 50\%$ covered at each of 3 elevations containing 50 squares each (ground: 0 – 1.0 m, low shrub: 1.0 – 2.0 m, high shrub: 2.0 – 3.0 m); to ensure horizontal measurements the observer squatted when reading the lowest level and stood while counting the 2 upper levels. In addition to forbs, shrubs, and saplings, we included any natural materials (e.g., tree trunk, log, boulder) that obscured the observer's view of the cover cloth and thus might provide concealment for a fisher. Cover measures were averaged both within and across height categories to represent each site.

Finally, measurements at the broadest (forest stand) scale were taken at each reproductive den following the standardized CSE protocol, a complex approach which we outline here only briefly (for a complete description see USFS 2013). We measured live trees within a variable-radius plot; we identified individual trees to measure with a Spiegel Relaskop (Relaskop-Technik, Salzburg, Austria) and a basal area factor of either 20 or 40 (depending on which was

best to sample trees at the site). For each tree we measured dbh, species, crown class, and height. We used fixed nested plots to measure snags, logs, seedlings, saplings, vegetation (shrubs, forbs, grasses), and fuels (duff layer, fine fuels; Fig. 3b); measurements of snags also included dbh, height, species, and decay level. Although we collected all data included in the full CSE protocol, our goal for this study was simply to characterize live trees, snags, and associated tree variables (e.g., basal area, stand density index). At fisher dens (both natal and maternal), we collected forest measurements within 5 clustered plots centered on the den tree (Fig. 3b). For the random plots, we used a subset of data collected by local USFS personnel in 2011 at randomly selected sites within the study area; these measurements were based on 3 plots, but occasionally data were available from only 1 or 2 plots (because these data were averaged, this discrepancy does not influence results). However, as the CSE plots were measured primarily to ground-truth LiDAR data, they covered a broader area than was typically used by our radio-collared female fishers. To compensate, we superimposed home ranges (95% kernel; see Green 2017) for all adult female fishers in our study, and we excluded all CSE plots that fell outside of the merged home ranges; additionally, we excluded 20 plots that were within 100 m of developed areas or within 50 m of a heavily trafficked road, had missing information, or were within 50 m of a fisher den. After exclusions, we used all remaining random plots which resulted in a sample size comparable to den plots. Plot data associated with reproductive dens of 3 females were excluded because comparable random plot data were not available within their home ranges. Elevation was similar among stands with fisher dens and available stands.

Data from the CSE plots were organized using USFS software. Data were entered to ExamsPC version 03.22.2015.2, consolidated into a database in FS Veg and summarized in Suppose (version 2.06), an interface for the Forest Vegetation Simulator (FVS; USFS 2016), to

calculate variables for analysis. FVS can calculate a wide variety of forest stand variables (Dixon 2002). We focused on calculations associated with stand conditions expected to be important to fisher habitat selection based on previous research, including basal area, large trees per acre, stand density index (see Barnes et al. 1998 for definitions), canopy cover, and stand tree height; we created variables associated with California black oak and large snags using minimum dbh measures. We selected 51 cm (20 in) and 61 cm (24 in) for minimum dbh thresholds for California black oak and 76 cm (30 in) and 89 cm (35 in) as thresholds for minimum dbh for snags and live trees as they represent a combination of relevant points for structures used by fishers (e.g., Purcell et al. 2009, Weir et al. 2012) and have relevance to local forest planning (see California Wildlife Habitat Relationship system, Mayer and Laudenslayer 1988; www.wildlife.ca.gov/Data/CWHR/Wildlife-Habitats). As the FVS model is known to underestimate canopy cover in the southern Sierra Nevada, we incorporated a script used by USFS silviculturists in this region to generate an adjusted estimate of canopy cover with our den and random stand data (pers. comm., R. Rojas, USFS, Prather, CA). We calculated elevation, slope, and aspect for den and random sites using a Digital Elevation Model at a 30m resolution in ArcMap10.1 (ESRI 2012, Redlands, CA); topographic variables were calculated for a 30m area to represent the stand with the den or the first random plot at the center.

2.5 Statistical analysis

To contrast microsites and structures used by fishers for resting and denning, we grouped data into 3 sets of comparisons: 1) resting locations of males versus those of females, 2) natal versus maternal dens of reproductive females, and 3) combined rest locations (males and females) versus combined den locations (natal and maternal) used by females. In summarizing data and conducting statistical comparisons, we included individual microsites or structures only

once per category (i.e., repeated use was excluded); however, we did calculate percent re-use within categories (e.g., natal den). We compared use for microsite types, structure types, and tree species with chi-squared tests; for continuous variables such as microsite height, structure height, structure dbh, decay, slope, and elevation we applied *t*-tests. For some comparisons, we used log or square-root transformation to reduce skew or to equalize variance. In a few cases where data transformation was not effective, we compared groups with non-parametric Mann-Whitney U-tests. We used a 1-tailed *t*-test to assess whether microsites (natural log-transformed data) were higher at natal and maternal dens found early in the season (March and April) than late maternal dens (May and June). We interpret statistical probabilities ≤ 0.10 as trends, and ≤ 0.05 as significant differences; where appropriate, we further adjusted our significance level using a Bonferroni adjustment.

To explore patterns in characteristics of forest features (live trees, snags, logs) used for resting and denning, we created 3 classification trees using the TREE package in R (version 3.2.3) and script modified from James et al. (2015). Our first classification tree used variables from rest structures with known microsites (males and females combined) to predict microsite type (cavity or platform). Our second tree used structure variables of dens to predict den type (natal or maternal). Our third tree used variables associated with rest and den structures in live trees, snags, or logs with known microsites to predict microsite type (cavity or platform). Classification trees were pruned to balance the lowest cross-validation error rate and interpretability (James et al. 2015).

To evaluate habitat selection by female fishers, we compared 1) den structures to available structures, 2) den sites to available sites, and 3) den stands to available stands. We summarized and compared individual variables selected *a priori* based on our understanding of

fisher habitat needs during reproduction and on previous studies (Zielinski et al. 2004a, Purcell et al. 2009, Weir et al. 2012) for descriptive purposes. In cases of high correlation (≥ 0.5) or functional redundancy we either picked a single variable or alternated use of variables in model creation. Measures of aspect were transformed into categories of northness and eastness using cosine and sine transformations, respectively (Clark et al. 1999).

We generated predictive models to evaluate the capacity of variables to predict potential fisher denning habitat, using the lme4 package in R with a logit function (Hosmer and Lemeshow 2000). Specifically, we created a set of 6 predictive model for den and random structures and a set of 10 models for den and random sites; we created a separate set of 15 predictive models for den and random stands. We included variables in models based on their relevance to our broader hypotheses, previous studies of fisher habitat use, and potential to complement each other relative to fisher ecology in a particular model; we focused on variables that reflected tree size, tree species, tree decay class, and cover. At the structure scale, we included either dbh or height in every model because they reflect tree size; we used dbh most often because potential den trees presumably need to be of a minimum diameter to be suitable for a fisher. Also at the structure scale, we included decay level, large broken limb, or live/dead to reflect potential presence of a cavity; while the presence or absence of a suitable den cavity might have provided greater accuracy in distinguishing trees suitable for denning from those that were not, assessing with certainty the existence or lack of a suitable cavity in random trees was not usually feasible. We included tree species or categories (i.e., hardwood) with potential to predict suitability for denning, with a focus on California black oak due to its value as a source of cavities in this region. At the site scale, we included arrangements of cover and topographic variables that might help illuminate whether cover, topographic features, or a combination of

both best characterized fisher denning habitat. Specifically, we included proximal canopy cover (0-15 m radius around tree) in most models because of its prevalence in previous fisher habitat studies. As we suspected understory cover might provide concealment for females as they travel to and from a den tree, we included a combined understory (0-3 m height) variable which might provide cover as the female climbs the den tree and a low understory (0-1 m height) variable which represented cover that might conceal a female on the ground. Further, we suspected that low understory cover might be more abundant at lower elevation sites in our area, so we included an interaction between low understory and elevation in models where they both occurred.

At the stand scale, we were guided by our hypotheses and previous fisher studies, but we also took into consideration variables that would be applicable to local foresters and managers using the FVS program. We included canopy cover in the majority of models due to its value in previous studies of fisher habitat. We included 1 of 3 variables associated with California black oak in most models instead of a broader hardwood category to improve interpretation of results and applicability to management; California black oak is the most common hardwood within the elevations of our study area and the dominant hardwood species used by fishers for resting in the southern Sierra Nevada (Zielinski et al. 2004a, Purcell et al. 2009). As the presence of a few California black oaks of sufficient size to contain a fisher-sized cavity may increase stand suitability for fisher reproduction, we used the variable trees per acre $\geq 24''$ in most models, but also included smaller trees per acre ($\geq 20''$) and basal area in other models for comparison. Large snags may be used as den structures, but may also reflect the age and decay level of a stand, characteristics relevant to suitability for denning; as such, we included basal area of large snags ($\geq 35''$) in many models, along with basal area of slightly smaller snags ($\geq 30''$) in 1 model for comparison. To represent other conditions of the stand, we alternated use of basal area (all

live trees), stand density index, large live trees per acre ($\geq 35''$), and tree height in models along with combinations of variables associated with canopy cover, California black oak, and large snags. We also included potentially influential topographic variables (elevation, slope, northness, eastness) in varying combinations in many models to allow for comparisons, with an emphasis on elevation (based on association with tree species distribution) and slope (based on previous studies).

Models were compared using Akaike information criterion values corrected for small sample sizes (AICc) and Akaike weights (w_i) calculated with the R package AICcmodavg (Burnham and Anderson 2002); to further assess model fit, we generated receiver operating characteristic (ROC) curves and calculated percent area under the curve (AUC). We present coefficients for the parameters in the top (most competitive) model for each comparison. Analyses were conducted in NCSS 11 (NCSS 2016) and R version 3.2.2 (R Core Development Team 2015).

3. Results

3.1 General summary of fishers captured and relocated while resting and denning

From June 2007 to December 2015 we captured and attached radio-collars to male ($n = 55$) and female ($n = 72$) fishers. We monitored all fishers year-round using ground telemetry through 2015, documenting males resting on 216 occasions with 9.3% reuse of structures and females resting on 824 occasions with 10.4% reuse of structures (Appendix B). We identified microsites of resting male fishers on 199 instances for males with 10.1% repeat uses and 763 instances for females with 10.7% repeat uses (Appendix B). Fifty-two females were monitored as adults for ≥ 1 spring denning season and 45 of these initiated natal dens in ≥ 1 year; over 8 reproductive seasons (2008 through 2015) we located 95 natal dens (8 of which appeared to fail

early) with 12.6% reuse of unique structures and 206 maternal dens with 14.0% repeat use of structures (Appendix B). We documented microsites of denning female fishers on 301 occasions, including 95 instances at natal dens and 206 at maternal dens (Appendix B).

Occasionally, reuse of individual structures occurred across groups, including 23 structures used by both male and female fishers for resting, 8 structures used as both natal and maternal dens, and 20 structures used for both resting and denning.

3.2 Microsites and structures used for resting and denning – assessing fisher habitat use

At the finest spatial scale, microsites used by fishers in our study area fell into 6 broad categories based on similarity of function and origin: cavity in standing tree, cavity in log, burrow, platform associated with a branch or branches, platform created by broken top of tree, and interstitial space (i.e., protected area within or under a combination of logs, rocks, or vegetation on the ground; Appendix A and B). For descriptive purposes, we also identified subdivisions of microsite categories when possible (e.g., type of branch platform; Appendix C). All cavity microsites occurred in boles of trees, with access points created predominantly by broken limbs, woodpecker holes, broken trunks, or cracks formed by damage (Appendix A). At a coarser spatial scale, structures used by fishers also fell into 6 general categories based on source and condition; these are live hardwood, hardwood snag, live conifer, conifer snag, hollow log (hardwoods and conifers combined), and other ground level structure (e.g., rock pile).

3.2.1 Rest locations used by male and female fishers

Male and female fishers used similar microsite types for resting, but at different frequencies ($X^2_4 = 33.84$, $P < 0.01$; interstitial spaces excluded due to low sample size; Fig. 4). Males rested in platforms formed by branches most often (38.5%), while females rested in tree cavities most frequently (47.0%; Fig. 4, Appendix B). Height of microsites used by males and

females did not differ (Table 2); this remained true if ground-level resting sites were excluded (males $11.6 \text{ m} \pm 6.5 \text{ SD}$, $n = 74$; females $10.8 \text{ m} \pm 7.0 \text{ SD}$, $n = 276$; $t_{348} = -0.85$, $P = 0.39$).

Male and female fishers used similar structure types for resting, but also at different frequencies ($X^2_5 = 14.40$, $P = 0.01$; Fig. 5, Appendix B). Males and females used live conifers (respectively 43.5%, 34.2%), live hardwoods (15.6%, 27.5%) and conifer snags (16.1%, 21.6%) more than any other structure types (Fig. 5, Appendix B). Fishers rested in 11 different tree species, although only 6 were used regularly; males and females differed in their use of these 6 species ($X^2_5 = 14.4$, $n = 840$, $P = 0.01$; Fig. 6). While proportional use differed somewhat between males and females, 3 tree species (white fir, ponderosa pine, and California black oak) accounted for the majority of species used by both males (77.2%) and females (77.7%; Fig. 6).

Fishers rested in structures that were large in diameter (Table 2, Appendix D). Males rested in larger diameter conifer snags and logs than those used by females (respectively, $127.2 \text{ cm} \pm 47.4$, $100.3 \text{ cm} \pm 28.5$; $t_{189} = -4.20$, $P < 0.003$), but for other structure types there were no such differences (live hardwoods, $t_{181} = -1.77$, $P = 0.08$; hardwood snags and logs, $Z = 0.21$, $P = 0.83$; live conifers, $t_{243} = 0.66$, $P = 0.51$; Appendix D). Male and female fishers rested in standing structures of similar heights (live hardwoods, $Z = 0.60$, $P = 0.55$; hardwood snags, $t_{18} = -0.17$, $P = 0.86$; live conifers, $t_{220} = 1.75$, $P = 0.08$; conifer snags, $t_{123} = 0.39$, $P = 0.70$; Appendix D). Both sexes rested in hardwoods with similar (and relatively low) levels of decay; decay class 2 was used most often (males 74.4%, females 68.8%), followed by class 1 (9.3%, 18.1%), and class 3 (7.0%, 6.0%; Appendix E). In conifers, males and females rested in structures with a wider range of decay, including in trees of class 1 most frequently (respectively, 43.6% and 33.1%), followed by class 2 (25.5% and 24.6%), and a mix of other classes with a peak around class 6 (10.0% and 15.5%; Appendix E). Male and female fishers rested on similarly steep

slopes (mean approx. 32.0%; Table 2); however, males used rest structures at higher elevations than females (male mean $1,602 \pm 302$, range 1039 – 2555 m versus female mean $1,524 \pm 232$, range 965 – 2227 m; $t_{255.3} = -3.15$, $P = 0.002$; Appendix D).

3.2.2 Natal and maternal den locations used by reproductive female fishers

All natal den microsites (100.0%) and nearly all maternal den microsites (99.0%; 2 late season exceptions were maternal dens in log cavities), were in tree cavities (Fig. 4, Appendix B). The entrances of natal den microsites showed a trend of being higher than those of maternal dens ($t_{237} = -2.08$, $P = 0.04$; Table 2). Additionally, den microsites located early in the season (March and April) were higher than those found later (May and June; $t_{259} = 3.92$, $P < 0.01$; Fig. 7a). Height of den microsites also varied with the selected structure type, and the pattern was similar for natal and maternal dens; microsite heights were generally highest in live conifers, then were progressively lower in live hardwoods, conifer and hardwood snags, then logs (Fig. 7b).

Reproductive female fishers used similar structure types for natal and maternal dens, but in different proportions ($X^2_3 = 8.14$, $P = 0.04$, Appendix B; excluding logs due to small sample size). Natal dens occurred in live hardwoods most frequently (45.8%), followed by live conifers (33.7%), and conifer snags (15.7%); maternal dens were also found most often in live hardwoods (55.2%), but then used conifer snags (26.6%) a little more than live conifers (20.3%; Fig. 5; Appendix B). Females used only 6 tree species as den structures (Fig. 6), and use of species did not differ between natal and maternal den structures ($X^2_4 = 2.92$, $P = 0.57$; excluding canyon live oak due to low sample size). For natal and maternal dens, female fishers used California black oak (49.4% and 56.8%, respectively) most often, followed by white fir (24.1% and 24.0%) and incense cedar (16.9% and 10.9%; Fig. 6).

Natal and maternal den structures were similar in terms of dbh (all P values > 0.21) and in height (all P values > 0.38 ; Table 2). As was the case for rest sites, hardwoods used as reproductive dens were most often in decay class 2 (natal 90.5%, maternal 92.6%), while conifers ranged over a greater variety of decay classes, with class 2 used most frequently for both natal (67.5%) and maternal dens (40.2%); the remaining conifers used as natal dens were nearly evenly distributed across classes 3-7 (Appendix E). Natal and maternal dens occurred on similarly steep slopes ($t_{270} = 1.04$, $P = 0.30$; Table 2) and at similar elevations (range for natal 1020 – 2059 m versus maternal 1013 – 2049 m; $t_{273} = -1.34$, $P = 0.18$; Table 2).

3.2.3 Rest locations used by both sexes relative to den locations used by reproductive females

Combined, males and females rested in a variety of microsite types including tree cavity (42.1%), branch platform (29.7%), and broken top platform (11.1%), whereas reproductive females denned exclusively in cavities (tree cavity 99.3%; log cavity 0.7%; Fig. 4, Appendix B). Of the microsites in standing trees, microsites used for resting were higher than those used for denning ($11.1 \text{ m} \pm 7.3 \text{ SD}$, $n = 350$ versus $9.8 \text{ m} \pm 7.8 \text{ SD}$, $n = 229$; $t_{573} = -2.25$, $P = 0.03$).

The proportion of structure types used for denning ($n = 267$) differed from those used for resting ($n = 910$; $X^2_5 = 90.24$, $P < 0.01$). Live conifers, live hardwoods, and conifer snags were the most widely used structures for both resting and denning; however, whereas live conifers were the most common rest structures, live hardwoods comprised roughly half of all den structures (Fig. 5, Appendix B). In contrast to conifers, we found few dens in hardwood snags. Resting fishers used a greater variety of tree species than did denning females, although California black oak and white fir were used more than any other species for both activities (Fig. 6). When comparing only species used > 5 times, proportions of tree species used for resting differed from denning ($X^2_5 = 68.39$, $P < 0.01$). Of note, California black oaks were used nearly

twice as often for denning compared to resting (respectively, 55.4% versus 29.9%); in contrast, ponderosa pine were used much more often for resting compared to denning (respectively, 18.6% versus 6.0%; Fig. 6). The other most commonly used species, white fir and incense cedar, were used at similar frequencies for resting and denning (Fig. 6).

Live conifers used for denning had greater dbh than those used for resting ($t_{292} = 4.21$, $P < 0.003$; Table 2, Fig. 8a), but this was not the case for other categories (conifer snags and logs, $t_{241} = -0.14$, $P = 0.89$; live hardwoods, $t_{315} = 0.14$, $P = 0.89$; hardwood snags and logs, $t_{35} = -0.55$, $P = 0.59$; Table 2, Fig. 8b-d). Mean diameter values were generally large for both rest and den structures across all tree species, although trees used for resting exhibited greater variability in size relative to den trees (Appendix F and G). Resting fishers (sexes combined) tended to use taller live hardwoods ($t_{296} = -1.78$, $P = 0.08$) and shorter conifer snags ($t_{176} = 1.63$, $P = 0.10$) than denning fishers, but height did not differ between the 2 groups for hardwood snags ($t_{28} = -0.72$, $P = 0.48$) or live conifers ($t_{269} = 0.31$, $P = 0.76$).

Resting and denning fishers used hardwoods in decay class 2 most frequently but they were much less flexible when denning (91.9% in decay class 2) than resting (69.7% class 2, 16.9% class 1). In contrast, conifer trees used for resting were most frequently in decay classes 1 (36.0%) or 2 (24.0%), while denning fishers used conifers in decay classes 2 most often (48.3%; Appendix E). Similar to comparisons above, all structures tended to occur on relatively steep slopes, although this was more pronounced for denning than resting fishers ($t_{876} = 4.50$, $P < 0.003$; Table 2). Finally, denning females showed a trend of using structures at lower elevations compared to resting animals (range for denning 1013 – 2059 m versus resting 965 – 2555 m; $t_{1162} = -2.67$, $P = 0.008$; Table 2).

3.2.4 Classification trees

The classification tree to predict use of cavities versus platforms in rest structures highlighted the important role of California black oaks in providing cavity microsites for resting (Fig. 9a). The overall tree had a misclassification rate of 18.1%, and indicated that California black oaks were associated with cavity microsites whereas a wide variety of tree species were commonly associated with platform microsites (Table 3). Among dead tree structures, logs were associated with cavities, while snags were often associated with either cavities (females) or platforms (males). The classification tree distinguishing natal versus maternal dens had a misclassification rate of 23.5% (Fig. 9b). Height of structures and slope influenced predictions in this second classification tree and interpretation was not straightforward; grouping of dens by tree height may have been associated with differences within tree species or decay level, but these two variables did not were not present in the pruned tree. Overall, trees shorter than 31.8 m tended to be maternal dens; on slopes < 33 degrees, natal dens tended to be both shorter and taller than maternal dens, and natal dens tended to occur on the very steepest slopes (> 61 degrees). Thus, in general, natal dens were often taller and on steeper slopes than maternal dens, but there were exceptions; the fine-tuning of height categories may be associated with difference in height of tree species (e.g., hardwoods versus conifers) or decay level in snags. The final classification tree contrasting cavity vs. platform use of rest and den sites combined had a misclassification rate of 14.9% (Fig. 9c). The most influential variable in this classification tree was decay level, with the first dichotomy distinguishing between live trees with little or no decay (class 1) and live trees or snags with increasing levels of decay (class ≥ 2). Rest or den structures with little decay were predicted to have platform microsites, with the exception of California black oak. Hardwoods in decay classes ≥ 2 were predicted to have cavity microsites; among

conifers with decay class ≥ 2 , males generally were associated with platform microsites, while females were associated with cavity microsites.

3.3 Comparison of reproductive dens and available habitat – assessing fisher habitat selection

Whereas results presented above compared microsites and structures in terms of their use by male and female fishers for resting, and by reproductive females as natal and maternal dens, here we focus at the structure and higher spatial scales and compare use to availability. Hence, this section directly addresses selection of features by fishers. Because some characteristics selected for by fishers differ qualitatively from those used (reported above), in some instances we note whether characteristics at natal and maternal dens differ.

3.3.1 Selection of den structures

We characterized structural features at 139 den trees (43 natal, 96 maternal) and 139 paired random trees (Table 4). As noted above, characteristics of structures used as natal dens did not differ from those used as maternal dens, further justifying our lumping of these groups into a single den category for comparison with available structures. Additionally, with few exceptions, attributes of structures used as dens (natal and maternal combined) were similar to those identified as random trees (Table 4). Live hardwoods selected for dens were larger in diameter than random hardwood trees ($t_{123} = -3.32, P < 0.01$), and live conifers used as dens were shorter than random conifers trees in the same stand ($t_{87} = 2.30, P = 0.02$). Tree species use differed between den and available structures ($X^2_3 = 10.85, P = 0.01, n = 273$; excluding tree species used ≤ 3 occasions); female fishers used California black oak and white fir more than expected, incense cedar in proportion to availability, and pine species (ponderosa and sugar pine combined) less than expected. Compared to available trees, den trees tended to have more cavities in boles (100.0% and 29.5%, respectively), more large broken limbs (54.7% and 39.6%),

more woodpecker activity (33.8% and 18.7%), fewer large dead limbs (51.1% and 60.4%), more broken tops (30.9% and 24.5%), and more major scars (27.3% and 22.3%; Appendix H).

3.3.2 Selection of den sites

Site level characteristics for den and random structures were similar (Table 4). Proximal canopy cover (0-15 m) was relatively high (ca. 72%) across all sites and did not differ between natal and maternal den sites or between all den and random sites (Table 4). Likewise, mean distal canopy cover (20-30 m) was comparable between natal and maternal dens (Table 4). In contrast, proximal canopy cover was greater than distal canopy cover across all dens ($72.1\% \pm 14.0$ versus $68.8\% \pm 15.7$; $t_{127} = 2.37$, $P = 0.02$). Understory cover (at 0-1 m, 1-2 m, 2-3 m) did not differ between natal and maternal den sites or between den and random sites (Table 4).

Because understory measures were similar, we also grouped these to a combined understory (0-3 m) variable for use in models; as with the separate analyses, the combined mean understory (0-3 m) was similar at den and random sites (Table 4). Measures of elevation, slope, and aspect (northness and eastness) did not differ between natal and maternal den sites, nor between den and random sites (Table 4).

3.3.3 Selection of den stands

We characterized 143 forest stands containing 48 natal and 95 maternal dens, and 145 random forest stands within the collective home ranges of reproductive female fishers (Table 5). Stands containing natal and maternal dens were similar in all metrics recorded, but den stands (natal and maternal combined) differed from random stands in several ways (Table 5). Specifically, fisher den stands had 14% denser canopy cover ($t_{286} = 4.44$, $P < 0.001$) and 45% higher stand density index values ($t_{286} = 8.44$, $P < 0.001$) relative to random stands. Fisher den stands also tended to have more large California black oaks per acre (and nearly twice the

density for oaks ≥ 24 in) as well as greater basal area of California black oak (all sizes), large snags (≥ 30 in and ≥ 35 in), and live trees (all sizes). Additionally, den stands were generally characterized by steeper slopes (21% steeper compared to random stands).

3.3.4 Predictive models

Structures. Our top model at the structure scale was moderately supported by AIC weight and ROC curve values ($w_i = 0.674$, AUC = 69.9%; Table 6). The top model for distinguishing den from random structures included dbh, decay, California black oak, white fir, incense cedar and large broken limb. Confidence intervals for variables did not overlap zero except for large broken limb (Table 7). The largest coefficients corresponded to presence of California black oak and white fir; dbh and decay may have exhibited less predictive power than expected because all random trees met minimum dbh and decay related criteria. The next best model based on AIC values contained all the same variables minus incense cedar and had a comparable AUC value (69.2%).

Sites. At this scale the most parsimonious model to distinguish den sites from random sites had relatively low support ($w_i = 0.281$, AUC = 57.7%). The model contained 5 variables including proximal canopy cover (0-15 m radius from tree), low understory (0-1 m height), elevation, slope, and the interaction between low understory and elevation (Table 4). Coefficients for all parameters were extremely small, however, and confidence intervals for canopy cover and slope overlapped zero, suggesting little or no ecological insight (Table 8). The next 3 models had comparable AIC weights (respectively, $w_i = 0.170, 0.154, 0.140$) and AUC values were low ($\leq 53.5\%$). Our findings at this spatial scale suggested that none of our models were able to strongly distinguish between den and random sites.

Stands. Of 15 models containing stand level variables, a single most-parsimonious model emerged overwhelmingly ($w_i = 0.998$, AUC = 85.2%; Table 8). Variables in this model included canopy cover, California black oak ($\geq 24''$) trees per acre, basal area of large snags ($\geq 35''$), stand density index, elevation, and slope; only confidence intervals for large snags overlapped zero (Table 7). However, most parameters were very small (<0.05); only trees per acre for large California black oaks (≥ 24 inches) appeared modestly important ($\beta = 0.26$). The next 4 models all had AUC values $\geq 81.4\%$; 3 of those models were variations on the top model, but with either slope, elevation, or both variables omitted. Interestingly, the remaining model with AUC of 81.8 % contained only stand density index, tree height, and all of the topographic variables (Table 8).

4. Discussion

Our investigation of fisher resting and denning habitat in the southern Sierra Nevada corroborates findings from previous studies and highlights the value of large trees and processes of decay in providing refugia for daily resting and annual reproduction for this rare species in forested habitats (Zielinski et al. 2004a, Weir et al. 2012, Gess et al. 2013). Our study was unique in several ways. First, we had the opportunity to contrast forest elements used by fishers for resting (both sexes) throughout the year with those used by females for denning (natal and maternal dens) in spring and early summer within the same geographic area. Second, because of the relatively long-term nature of our project, we were able to monitor quite a few individual animals, track some females over multiple years of reproduction, and document a considerable number of microsites and structures used by fishers across our study area. And third, we had the opportunity to compare habitat used by female fishers for denning to available habitat at several spatial scales. Descriptions of the microsites and structures used by fishers for resting and denning can provide guidance for managers overseeing forested landscapes in this region.

Resting fishers in the southern Sierra Nevada frequently relied on forest elements that take time (and decay) to develop (e.g., large live trees with cavities or platforms, large snags with cavities or broken tops, large hollow logs), but they also took advantage of other options such as younger conifers with suitable platforms and burrows in boulder piles; in contrast, reproductive females specialized on large diameter trees with cavities of sufficient size to rear young. Our assessment of habitat selection identified key attributes of structures, sites, and forest stands selected by females for denning relative to available habitat that have not been previously documented in the southern Sierra Nevada; our findings reiterated that a combination of large diameter live trees (particularly California black oak), large diameter snags, dense canopy cover, and decay are important components of fisher denning habitat in this region. Although the close affiliation between fishers and features of older trees and forests has been documented previously (e.g., in British Columbia; Weir et al. 2012), our findings underscore that these features remain key to supporting fisher reproduction in the more xeric conditions of the southern Sierra Nevada.

4.1 Fine scale habitat used for resting compared to denning

4.1.1 Microsites

Observations in our study and previous research suggest that the presence of fine-scale features suitable for use as microsites influence fisher selection of structures. Features used as rest or den microsites by fishers in our study provided refuges with comfortable space (i.e., suitable area and substrate), physical protection, and visual camouflage (Appendix A). We found no evidence that fishers created their own rest or den microsites; instead, they relied on ecological processes to form these features. Factors such as decay, excavation by woodpeckers, fungus, rust, insects, fire, and physical damage contribute to the creation of cavity and platform microsites (Laacke and Fisk 1983, McDonald 1990). Tree cavities are often formed by fungal

activity and associated heart rot, processes affected by climate and susceptibility of tree species (Oliver and Larson 1996, Remm and Löhms 2011); large dead limbs or other damage may provide entrance points for fungal spores that can lead to heart rot (Laacke 1990, Oliver and Larson 1996). In the Sierra Nevada, heart rot can affect conifer species but is more commonly observed in hardwoods such as California black oak (Laacke and Fisk 1983, McDonald 1990); based on extensive hollows, log cavities used by fishers were almost certainly derived from trees that experienced heart rot while standing and retained useable cavities after falling (R.E.G., pers. obs.; see also Oliver and Larson 1996, Ranius et al. 2009). Fishers also relied on natural processes (e.g., broken limb, pileated woodpecker excavation; Bonar 2000) to develop access points to tree and log cavity chambers. Maintaining natural processes and the ecological pathways that promote the creation of various microsite types is important for fishers, and beneficial to other wildlife species that utilize cavities (Bunnell 2013).

Contrary to our first hypothesis (H1), both male and female fishers used a variety of microsite types when resting (Fig. 4, Appendix B). In agreement with our second hypothesis (H2), females relied almost exclusively on cavities in standing trees for den microsites, with the only exceptions being 2 late season maternal den microsites in log cavities (Fig. 4, Appendix B). Thus, as in other geographic areas, tree cavities appear to be an essential habitat element for fisher reproduction in the southern Sierra Nevada (Fig. 4; Paragi et al. 1996, Powell et al. 2003, Weir et al. 2012). Tree cavities used by fishers seemed to offer greater protection from abiotic and biotic elements than other microsite types. Fishers of both sexes rested in tree cavities, but females used these features more often than males (Fig. 4). Females are smaller-bodied than males (Powell et al. 2003), thus cavities may offer increased physical security or buffer the effects of cold conditions (Maziarz and Wesołowski 2013, Thompson and Purcell 2016, Green

2017); moreover, the larger body size of males (e.g., broader head and girth) may prevent them from using some tree cavities that are accessible to females (Green 2017). Females may also rest in cavities to gauge conditions (e.g., thermal properties, presence of fleas, use by other animals) of potential future den microsites. In general, cavities in logs used by fishers appeared to have larger entrances and greater floor space than cavities in standing trees due to the horizontal position of the hollow; these characteristics might increase suitability of log cavity microsites for large males and females with mobile kits in the summer. The tendency for females to select higher microsites for dens initiated early in the season (Fig. 7a) may reflect greater safety from predators or increased solar exposure during daylight hours (to warm young kits, especially when the female leaves the den to hunt); later in the season, females may have selected lower entrances to facilitate moving large unwieldy kits and minimize accidents as kits began to climb on their own. Similarly, many bird species experience higher fledgling survival with higher nest placement, including species using tree cavities (Li and Martin 1991, Fisher and Wiebe 2006, Cockle et al. 2015).

Platform microsites used for resting that were associated with branches or broken tops of trees provided elevated refuges where fishers were obscured from view due to the cupped shape of the features and the cryptic coloration of their fur (Appendix A). Branch clusters (or brooms) used as microsites formed a matted or intertwined group of branches large enough to hold a fisher; known causes of brooms include disease (fungi, rusts), parasites (dwarf mistletoe), and other organisms (Tinnin et al. 1982, Tinnin and Forbes 1999). Stick nests consisted of a combination of pine needles, deciduous leaves, or sticks that may have been created by animals (e.g., squirrel, small raptor) or an accumulation of litter caught in a branch or adjacent to the trunk. Individual branches (not clusters) used by fishers generally were wide (≥ 12 cm) and thus

associated with large old trees. Broken tops used by fishers in live trees and snags contained flat areas where fishers could hide from view in a depression rimmed by bark, decaying wood, or live foliage; trees had to be of large diameter with significant decay for fisher-sized broken top platforms to develop. Platform microsites appeared to be difficult for known local predators (e.g., mountain lion, *Puma concolor*; bobcat, *Lynx rufus*) to access and offered other benefits such as exposure to solar radiation on cool days, access to breezes on hot days, and hidden vantage points from which to observe predators or prey on the ground (R.E.G., pers. obs.).

While used somewhat infrequently, ground burrows appeared to be important in some situations (e.g., females with kits in summer, males in habitat patches with limited tree microsites). Burrows appeared to be formed by natural forces outside of the scope of forest management, including spaces created by boulders, caverns formed by water flow, or tunnels created when large roots had decayed or burned; we rarely found fishers in our study area using burrows formed only from snow, although we did find them inside hollow logs that were partially or entirely covered with snow. Females with semi-mobile kits may have selected burrows in summer due to accessible entrances and (potentially) spacious interiors. Two relatives of the fisher in North America, the wolverine (*Gulo gulo*) and American marten (*Martes americana*), have also been documented using microsites that would fall into our burrow category when rearing young (Magoun and Copeland 1998, Ruggiero et al. 1998); in particular, wolverines will den in snow burrows (or tunnels) which can also be associated with boulders or fallen trees (Magoun and Copeland 1998), while martens have been documented using spaces within rock piles and underground burrows (Ruggiero et al. 1998, Erb et al. 2013). Although wolverine and American marten both appear to use burrow-type microsites more regularly than fishers, this shared pattern of use during portions of the kit rearing process suggest these features

provide similar benefits to females with young. Anecdotally, field experience in our study suggested that burrows may maintain cool temperatures even on hot days; further study is needed, but if summers in this region become increasingly warm and dry (as predicted; Diffenbaugh et al. 2015), burrows may be of unique value as cool refugia for resting fishers.

4.1.2 Structures

Conservation of fisher habitat often relies on data from the structure spatial scale to inform forest management. In the southern Sierra Nevada, structure types used for resting by both sexes were largely similar in size (Appendix D), with the exception that males generally used larger diameter conifer snags and logs than females, perhaps due to their larger body size. Another exception was that live conifers used for denning typically were larger (dbh) than those used for resting, supporting our third hypothesis (H3); this finding may simply reflect the fact that large cavities (for dens) require large trees, while resting fishers also used platforms on branches of trees that could be variable diameter. Trees used as rest and den structures also exhibited different patterns of decay; fishers often used live trees with little decay (class 1) for resting, whereas den trees generally had higher levels of decay. Both rest and den structures occurred on steep slopes, although this was somewhat more pronounced at dens; dens on steep slopes may offer more favorable microclimates due to increased solar radiation or alternatively, large old trees may be more common on steep slopes in our study area due to past management activities (i.e., trees were not easy to access with logging equipment).

Hardwoods (dominated by California black oak) accounted for roughly half of all reproductive den structures and a quarter of all rest structures in our study area (Fig. 5); fishers used California black oak and, to a lesser extent, white fir, for denning out of proportion to availability, and appeared to avoid pines for denning compared to available (Table 4). This

finding also supported our third hypothesis (H3) that females would favor hardwoods for den structures (see also Paragi et al. 1996, Weir et al. 2012). Live trees may provide greater physical security and insulation compared to snags or logs (e.g., Cockle et al. (2015) documented higher nest survival for large birds using cavities in live trees compared to snags and Coombs et al. (2010) showed that large live trees with limited decay buffered cold nighttime temperatures better than snags with more decay). Moreover, unpublished data from the CSE plots conducted in our study area indicated that hardwood snags were uncommon compared to live hardwoods, suggesting that hardwoods with extensive hollows might spend little time standing as snags. Notably, heartwood decay is initiated only in living trees, so decay must occur before a tree dies for a large hollow to form; older trees are more susceptible to heart rot than younger trees, and hardwoods tend to be more susceptible than conifers (Oliver and Larson 1996, Bunnell 2013).

Conifers comprised the other half of the den structures used. Females selected live conifers somewhat more often than snags as natal dens, possibly because live trees offered higher levels of physical and thermal protection for young kits (Cockle et al. 2015). In contrast, females increased their use of conifer snags and live hardwoods relative to live conifers for maternal dens (Fig. 5); conifer snags with extensive decay may have lower cavities or larger interior chambers, traits potentially useful to females at maternal dens when kits have grown in size. Male and female fishers rested in live conifers more frequently than in conifer snags, and both sexes used conifer logs, although somewhat infrequently. The conifer species used most often for denning were (in order of frequency) white fir, incense cedar, and ponderosa pine; for resting, the most common conifers were white fir, ponderosa pine, then incense cedar (Fig. 6). At least to some extent, patterns of use for individual tree species may reflect local availability; for example, large diameter ponderosa and sugar pines have been selectively removed from

Sierra Nevada forests in many areas, but they may have played a more important role as sources of cavities when large pines were more common elements of these forests. Alternatively, they may indicate differences in capacity to develop types of microsites (i.e., cavities versus platforms), or persist over time; specifically, white fir may be more prone to developing cavities than other local conifers because of susceptibility to heart rot (Laacke 1990) and individual incense cedars with cavities may remain available for a long time because of high resistance to decay (McDonald 1973). Conifers used for denning spanned a narrower range of diameters and were larger in diameter compared to those used for resting, likely because all trees used as dens contained a large cavity in the bole while trees used for resting could be associated with a variety of microsites – including branch clusters in potentially smaller diameter trees; this finding emphasizes that while smaller (younger) conifers may be useful for resting, large decadent trees are still essential for denning.

In our study area, standing trees (both live and dead) comprised the majority of rest and den structures. Use of large logs (hardwood and conifer) with hollows for resting was less common (Fig. 5) but they may still provide important functions. Opportunistically, we documented family groups using hollow logs as maternal rest structures in summer and fall with remote cameras; females sometimes used the same logs for multiple days or on separate occasions. Less frequently, fishers used sheltered spaces under suspended logs, naturally formed log piles, and human-created slash piles. Notably, the slash piles used by fishers were quite large; as examples, 2 piles composed of small diameter trees were about 5 m tall, and were 13 x 29 m and 33 x 51 m in area, respectively. Where forest management activities such as thinning are planned and other rest structure options may be limited, leaving large hollow logs or log piles with protected interstitial spaces could enhance the area for fishers. Last, the burrows used by

fishers in our study area were generally associated with rocky outcrops, clusters of boulders in dry stream beds, or decayed stumps. While these elements cannot be managed in the same manner as trees, recognizing that they have some value to fishers could help inform management decisions related to connectivity in areas where large tree structures are limited.

4.1.3 Intersection between microsites, structures, tree species, and time

Tree species differ in their ecology, distribution, patterns of growth, and vulnerability to decay (Oliver and Larson 1996); correspondingly, the trees used by fishers in our study area seemed to vary in the resources they offered for resting or denning. Of the hardwoods, California black oaks were conspicuous as a source of tree cavities with characteristics suitable for fishers (e.g., appropriate size, depth, and insulation; Table 3). In comparison, we infrequently found fishers in cavities of canyon live oak, and we suspect this species did not generate as many suitable cavities in our study area, possibly due to small diameters or resistance to heart rot; therefore, while our study reinforced the importance of hardwood species for denning and resting, these data also underscore that some hardwood species were of greater value to fishers in providing cavity microsites. Many of the oaks with cavity microsites used by fishers were decadent trees with large hollows that may have limited time remaining as standing trees. Hollows typically form only after many years in oaks; in Sweden, only 1% of pedunculate oaks (*Quercus robur*) < 100 years old had hollows, whereas 50% of trees 200 – 300 years old contained hollows, and all trees > 400 years old had hollows (Ranius et al. 2008). We are unaware of data on how long it takes for hollows to form in California black oaks, but this emphasizes the exceptional amount of time that may be required to form structures with cavities suitable for fishers. Fast growing pedunculate oaks also grew larger limbs and formed hollows at younger ages than slower growing trees (Ranius et al. 2008); fostering rapid growth of California

black oaks that have a good chance of developing suitable hollows could be an important step towards recruiting den structures that can replace existing trees in the future in this region.

In contrast to hardwoods, multiple conifer species were used regularly by fishers (Fig. 6); specifically, white fir and incense cedar were used most often for denning, while ponderosa and sugar pine were used more often for resting. White firs were widespread at higher elevations in our study area and provided fishers with both cavity and platform microsites. Fishers used branch platforms in ponderosa pines much more frequently than cavities (Table 3), suggesting that this species did not readily generate large cavities or available trees were of insufficient size or decay level to contain cavities in our study area. Sugar pines showed a similar pattern to ponderosa pines, but supplied proportionally more cavities (Table 3). Fishers found in incense cedars generally were using tree cavities; we also found fishers in log cavities of incense cedar more than any other tree species (Table 3). The wood of incense cedar is very hard and known to resist decay; incense cedar with hollows may therefore be more likely to stay intact when they fall and last longer as logs than some other conifers (McDonald 1973).

4.2 Habitat selection by denning female fishers across 3 spatial scales

4.2.1 Structures

The above results provide metrics on use for resource managers, but they cannot be used to infer selection of given features without placing these in the context of the availability of these features. At the structure scale our results supported our hypothesis (H6) that reproductive females would favor large diameter trees and hardwood species (specifically, California black oak) for denning (Table 4). Notably, hardwoods used as den structures were significantly larger than available hardwoods; while this was not true for conifers selected for denning, they were shorter on average than random trees, possibly due to more advanced decay. The top models to

describe trees used as dens included positive coefficients associated with California black oak, white fir, incense cedar, and large broken limbs (Table 6 and 7); these findings complement our descriptive results, as these species were used most often as reproductive dens, and broken limbs could reflect decay associated with the presence of a cavity.

4.2.2 Sites

Canopy cover is known to be an important component of fisher habitat (Zielinski et al. 2004a, Purcell et al. 2009). We also anticipated understory cover (either low 0-1m or combined 0-3m height) to be of value to females traveling to and from the den to minimize risk of detection by larger carnivores known to prey on fishers in our region (Wengert et al. 2014). We therefore expected (H7) fishers to select sites with denser tree canopy and understory cover relative to available sites; instead, we found that mean values of tree canopy cover to be high and virtually identical across sites, while understory cover was comparably dense at den and random sites (Table 4). Moreover, data collected at the site scale revealed no real differences between variables measured at dens and available sites (Table 4). Top models at this scale included cover-associated parameters (as predicted by H7) to influence site selection, but even the best model was not well supported (Table 6). We suspect that females selected forest stands with high levels of cover, resulting in sites within the stand being very similar. Canopy and understory cover also were similar and relatively high at both types of den sites (natal and maternal) and we rejected our hypothesis (H5) that proximal canopy cover would be lower than distal cover to increase the interception of solar radiation at the den. To ensure that measurements were recorded consistently and that they were compatible with measurements collected by local foresters, we measured canopy cover at all dens in summer when deciduous trees are leafed out; consequently, hardwood canopy cover may have been overestimated relative

to what would have been present when females selected and initially used den locations; future research efforts could explore this possibility. Finally, topographic variables (i.e., aspect, slope, and elevation) were similar at den and available sites.

4.2.3 Stands

Finally, findings at the stand spatial scale, including variables in the top model, provided support for our final hypothesis (H8); forest stands with fisher dens tended to have higher canopy cover, a higher number of large (≥ 61 cm) California black oaks per acre, greater basal area of California black oaks, greater basal area of large (≥ 89 cm) snags, and higher stand density indices compared to available habitat (Table 5). Additionally, den stands occurred on somewhat steeper slopes and slightly lower elevations than random stands within our study area. California black oak was an important source of den microsites in our study; thus, it seems plausible that the presence of 1 or more large California black oaks with cavities could influence whether or not a stand is suitable for denning. Large snags might also be of value because they contain suitable cavity microsites, but they may also simply reflect other relevant characteristics such as the age and prevalence of decay in a stand. Stand density index was included in the top 5 models, suggesting this measure may have some capacity to identify stands potentially suitable for denning. Stand density index combines tree diameter and tree density, thus may better reflect conditions present in forest stands of value to fishers than basal area or tree density alone; in support of this idea, Lilieholm et al. (1994) highlighted the benefits and application of stand density index to manage forest stands at goshawk nests. Additional explanations for females selecting stands with higher values for metrics for California black oak (basal area, number of trees per acre), basal area of large snags, and stand density index include availability of other potential den structures, multiple escape options, or stable thermal conditions.

Fishers have been associated with high levels of canopy cover in many studies, so dense tree canopy in the forest around fisher dens corresponds with known habitat preferences. Dense canopy cover in the den stand may contribute to concealment as females travel to and from their dens each day, but may also create desirable thermal conditions (Barrows 1981, Matlack 1993). It is worth noting that the adjusted canopy calculation that we used in FVS yielded mean canopy cover estimates that were higher than the original estimates for both den (77.2% versus 64.8%) and random stands (67.8% versus 56.7%), although increases were comparable for both groups. Steeper slopes may give females a better vantage as they leave dens or increase their safety in other ways; alternatively, if steeper slopes hindered historic logging activities, then stands of older and larger trees may have been disproportionately left on steep slopes in some areas. Finally, it is worth noting that California black oak occurred across the elevation range occupied by females in our study area, but this species was more common at lower elevations; thus, the inclusion of elevation in models may reflect regional distributions of tree species. As has been suggested previously by Zielinski et al. (2004b), the presence of California black oaks may influence where female fisher establish home ranges in the southern Sierra Nevada due in part to their importance to potential prey (e.g., animals that eat acorns or use cavities), value as structures for resting (Zielinski et al. 2004a), and as we have documented in this paper their significance as potential den structures.

5. Conclusions

Roughly a century of fire suppression, timber harvest, and development across forests in the western United States has led to changes in species composition, size classes, and availability of large decadent trees (Parsons and DeBenedetti 1979, Ansley and Battles 1998, Scholl and Taylor 2010). In recent years, drought conditions and beetle outbreaks have led to extensive tree

stress and mortality in the Sierra Nevada (Miller and Stephenson 2015, Asner et al. 2016, VanMantgem et al. 2016, Young et al. 2017); the short and long-term impacts of this ongoing phenomenon on forests and fisher habitat remain uncertain. In the face of such concerns, we outline some points we believe important in managing forests in this region to maintain habitat that can support reproduction and resting activities of fisher. First, retention of large diameter live trees and snags (Table 2, Appendix D, F, and G) with some level of decay will improve the availability of rest and den structures; if individual structures need to be selected, we suggest prioritizing trees with signs of suitable cavity microsites (e.g., large broken limbs, pileated woodpecker holes) or other potential microsites (Appendix C). Retention of large hollow logs may provide structures of use to reproductive females with mobile kits and large males. Second, the development of long-term plans to recruit and replace existing structures is needed as they will eventually be lost to decay or other factors; recruitment may be especially important in places where large diameter trees are limited or may be lost in the near future. Third, some tree species warrant greater consideration and prioritization in plans to protect or recruit den and rest structures. California black oak and white fir were used in greater proportion to their availability for dens, while incense cedar was used in proportion to availability; these species may simply be the most likely to develop suitable cavity microsites. Thus, maintaining a well-distributed supply of large diameter trees of these species may help ensure availability of den structures (as well as rest structures with cavity microsites). California black oak and incense cedar also have greater drought tolerance than some species, which may prove beneficial under predicted warmer and drier climatic conditions (McDonald 1990, Powers and Oliver 1990, Mann and Gleick 2015). Ponderosa pine, sugar pine, and canyon live oak trees are also of value to fishers, but our findings suggest that available trees in this region are more likely to provide microsites and

structures for resting than denning. Fourth, cover at den sites did not differ from that at available sites; rather, values were high across locations. Consequently, retaining dense canopy cover and moderate understory cover around large structures when feasible will likely improve fisher habitat suitability for denning (Table 4). Fifth, knowledge of conditions found in known den stands can suggest characteristics useful for management; relative to available stands, den stands in our study had higher density and basal area of large California black oaks, higher basal area of large snags, higher stand density indices, denser canopy cover, and steeper slopes (Table 5).

As forests in the southern Sierra Nevada continue to respond to extrinsic stressors (air quality, climate change, etc.), we need to balance protection of existing old forest structures and stands with recruitment of future habitat suitable for denning and resting by fishers; focusing on both retention and recruitment of California black oaks may be especially beneficial to fisher reproduction in this region and potentially contribute to more resilient forests. Most of the microsites and structures used by fishers for resting, and virtually all those used for denning, require extensive time and a unique series of ecological processes to develop; thus, they cannot be easily or quickly replaced if lost (Manning et al. 2013). We did not determine the age of the trees used in our study, but other resources can put the potential age of these trees in perspective. McDonald (1990) calculated that California black oaks with a dbh of 61 cm were around 150 years old and trees with dbh of 81 cm were near 200 years old. The mean dbh for hardwood trees used as dens in our study was 75.7 cm; considering the additional time needed to develop large cavities, many of the den trees in our study could have been at least 200 years old. Conifer structures, particularly large snags, may take as long or longer to reach a size and decay level usable for denning female fishers (McDonald 1973, Parker and Peet 1984). Further study is

needed to clarify ages at which different tree species are likely to yield potential den or rest structures for use in local forest plans.

Understanding fisher ecology and behavior provides insight into the factors underlying habitat use and selection. Fishers in our study area used a variety of microsite and structure types for resting, but these diverse habitat elements almost always provided visual camouflage and physical or thermal shelter. Male and female fishers exhibited many similarities in the rest locations they used, with most differences potentially explained by sexual dimorphism in body size. In contrast, reproductive females require cavities in standing trees for denning, presumably because they provided the requisite physical and thermal protection for kit rearing (Green 2017). Decisions by fishers to use specific rest or den locations are certainly influenced by habitat characteristics, but may also be influenced by other fishers (Green 2017) or co-occurring species (Benson et al. 2006, Jachowski et al. 2011, Fisher et al. 2013). Observations of den cavity entrances during litter counts suggest that female fishers may choose natal den microsites with entrances that restrict entry by males during the mating season and they appear to avoid choosing den structures too close to neighboring reproductive females (Green 2017, Green et al. 2017a). The spatial (and likely temporal) distribution of favored sites for reproduction may also be influenced by occurrence of competitors that use cavities (e.g., American marten (*Martes americana*), ringtail (*Bassariscus astutus*; Zielinski et al. 2005), prey species (e.g., gray squirrel (*Sciurus griseus*), Douglas squirrel (*Tamiasciurus douglasii*; Zielinski et al. 1999), avian cavity excavators (e.g., pileated woodpecker; Bonar et al. 2000), and known predators (e.g., bobcat, mountain lion; Wengert et al. 2014). Ultimately, the reproductive niche of fishers is complex and responsive to many extrinsic factors. Finally, fisher use and appear to favor forest features that are likely to be of high value to other species. If they do serve as an effective management

umbrella species (Caro 2010), then conservation efforts that support fisher reproduction in this region is likely to help sustain a broad community of plant and animal species associated with older trees and forest.

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Table 1. Description of terms associated with habitat used by fishers (*Pekania pennanti*) for resting and reproduction at distinct spatial scales. Some terms are revised from previous studies within the *Martes* complex (e.g., Zielinski et al. 2004a, Weir et al. 2012) based on observations made during this study. See Slauson and Zielinski (2009) for a diagram depicting spatial scales noted in the table: microsite (which they refer to as location), structure, site, and stand.

Term	Description
Resting	Periods of inactivity by male and female fishers throughout the year. Resting typically occurs in secluded places that change on a daily basis. Locations used for resting may also provide a buffer to inclement weather, refuge from predators, and shelter in which to consume prey.
Denning	Periods of inactivity and maternal care during spring and early summer by adult female fishers with young. Denning occurs in secluded places that are used repeatedly (i.e., from a few consecutive days to > 1 month).
Den	The location where kits are housed and cared for by their mother. We refine “den” with spatial terms to indicate the scale of interest (e.g., den microsite, den structure). In the field, dens were usually identified by female re-use of locations during known periods of reproduction (early March – late June); a location was considered a den if a female used it for ≥ 2 consecutive days, or on multiple occasions over a week, or if kits were documented.
Natal Den	The place where a reproductive female fisher gives birth (parturition) and cares for new-born kits.
Maternal Den	The place used by a reproductive female with dependent kits after the natal den, but while kits are still nursing and largely dependent on the mother for transport.
Microsite	The specific location and feature in or on a structure (see below) used by a fisher for concealment, comfort, and protection from abiotic (e.g., temperature) and biotic elements (e.g., predators). Fishers do not create microsites, but rely on natural processes and other species for their formation.
Rest Microsite	The specific fine scale location of an inactive male or female fisher; this includes cavities and platforms (branch clusters, large branches, nests, broken tops) in live trees and snags and ground level features like hollows in logs, burrows in ground, rock, or snow, and interstitial spaces in structures like log piles.
Den Microsite	The specific fine scale location within a structure where a reproductive female rests, tends young, and leaves kits when gone; this includes cavities in live trees or snags and, on occasion, cavities in logs.
Structure	The specific physical structure within which a rest or den microsite is located. Most structures used by fishers are a form of tree (live, snag, log), but other ground level structures (or substrates) may be used (e.g., rock piles, ground caverns, slash piles, natural log piles).

Rest Structure	The physical structure in which a fisher is (or was known to be) resting. Fishers require microsites of large size compared to many other highly arboreal species in North America, so trees used as rest structures often are correspondingly large with attributes that facilitate the formation of suitable microsites (e.g., large limbs, decay, woodpecker activity, rust). Ground-based structures may be used but these also must be of adequate size and stability to contain a suitable microsite.
Den Structure	The physical structure in which a fisher keeps (or was known to keep) dependent kits. Reproductive females use standing trees with cavities in the bole almost exclusively for denning, thus they require large trees with a sufficient level of decay or excavation as den structures.
Rest or Den Site	An area encompassing a rest or den microsite, structure, and a small radius around both; in this study, we used a 15m radius circle. The site contains understory and tree cover proximate to the structure which may influence local thermal conditions and opportunities for concealment.
Rest or Den Stand	A relatively uniform patch of forest within which a rest or den structure is located. Stands have been defined as sub-communities or local patches delineated based on homogeneity of tree age, structure, and species relative to the surrounding forest (Ford-Robertson 1983); as such, stand size often is not standardized. In our study, we used a cluster of 5 plots within a 56.6 m radius of the structure to represent den stand conditions.
Mobile Kit Rearing	The period of time during the summer and early fall when reproductive females are raising kits that are increasingly mobile, but still learning to hunt, climb, and travel.
Maternal Rest Structure (Microsite, Site, or Stand)	A place used by reproductive females with mobile kits after maternal dens, but prior to kit independence during mid- summer and early fall. Kits may be left at these sites while the female hunts. As with den or rest locations, additional terms can indicate the scale of interest.

Table 2. Characteristics of fisher habitat at microsites and structures used for resting and denning on the Sierra National Forest (2007—2015. Tree measurements were subdivided into hardwood and conifer species, and live or dead structures, due to potential differences between these categories. See Appendix D for data associated with individual sexes and Appendix F and G for diameters of individual tree species. Microsites or structures used on > 1 occasion were counted only once per category. We used a Bonferroni-adjusted P value of 0.003 for significance, reflecting an alpha of 0.05 and 18 tests; bold letters denote statistical differences. Despite not meeting the criteria for statistical significance, height of all natal den microsites showed a trend of being higher than maternal den microsites ($t_{236} = -2.034$, $P = 0.043$) and rest structures tended to be at higher elevations than den structures ($t_{1162} = -2.649$, $P = 0.008$).

Habitat Characteristics	Rest Microsites and Structures	Den Microsites and Structures		
	Mean \pm SD (n)	Mean \pm SD (n)		
	Sexes Combined	Natal	Maternal	Dens Combined
Microsite Height (m)				
All (tree, ground)	8.8 \pm 7.8 (443)	11.2 \pm 9.3 (67)	9.1 \pm 6.9 (171)	9.7 \pm 7.8 (231)
Hardwood – Live	7.1 \pm 5.5 (131)	6.8 \pm 2.4 (33)	6.7 \pm 3.5 (94)	6.7 \pm 3.3 (125)
Hardwood – Snag	5.6 \pm 2.5 (15)	4.5 \pm 2.3 (3)	7.0 \pm 3.2 (6)	6.1 \pm 3.1 (9)
Conifers – Live	16.7 \pm 6.9 (116)	18.5 \pm 12.2 (22)	16.7 \pm 10.2 (29)	17.9 \pm 11.1 (48)
Conifer – Snag	10.4 \pm 5.5 (88)	12.0 \pm 7.8 (9)	10.0 \pm 6.4 (40)	10.4 \pm 6.7 (47)
Structure Height (m)				
Hardwood – Live	20.4 \pm 8.0 (161)	18.9 \pm 5.3 (38)	19.0 \pm 6.7 (101)	18.9 \pm 6.4 (137)
Hardwood – Snag	11.2 \pm 4.9 (19)	9.8 \pm 4.9 (4)	10.1 \pm 3.7 (7)	10.0 \pm 3.9 (11)
Conifer – Live	38.2 \pm 11.2 (211)	40.0 \pm 9.0 (28)	37.8 \pm 10.3 (36)	38.7 \pm 9.8 (60)
Conifer – Snag	16.7 \pm 10.6 (121)	22.7 \pm 13.7 (13)	19.3 \pm 12.2 (46)	20.2 \pm 12.6 (57)
Structure dbh (cm)				
Hardwood – All	76.4 \pm 20.6 (205)			75.7 \pm 18.3 (149)
Hardwood – Live	76.6 \pm 20.5 (180)	79.1 \pm 20.6 (38)	75.0 \pm 17.7 (101)	76.3 \pm 18.6 (137)
Hardwood – Snag/Log	74.4 \pm 21.8 (25)	62.6 \pm 6.0 (4)	72.5 \pm 14.0 (8)	69.2 \pm 12.6 (12)
Conifer All	99.6 \pm 34.5 (418)			109.2 \pm 27.3 (118)
Conifer – Live	94.9 \pm 33.6 (234)	115.6 \pm 27.7 (28)	111.5 \pm 20.4 (36)	113.4 \pm 24.3 (60)
Conifer – Snag/Log	105.5 \pm 34.8 (185)	108.3 \pm 32.2 (13)	103.4 \pm 28.6 (47)	104.8 \pm 29.6 (58)
Topography at Structure				
Elevation (m a.s.l.)	1541 \pm 250 (898)	1520 \pm 230 (83)	1480 \pm 224 (192)	1494 \pm 227 (267)
Slope (%)	32.0 \pm 17.6 (616)	35.1 \pm 16.0 (82)	37.3 \pm 16.0 (190)	36.6 \pm 15.9 (264)
Aspect (degrees)	188 \pm 96 (657)	204 \pm 97 (82)	190 \pm 99 (190)	195 \pm 97 (264)

Table 3. Distribution of microsite types within tree species used as fisher rest structures and reproductive den structures (natal and maternal dens combined). Microsites used on > 1 occasion by a fisher were counted only once per category and only tree species associated with ≥ 5 microsites were included. California black oak was disproportionately used by fishers for tree cavities, while branch platforms and stick nests were frequently used in ponderosa pine.

Microsite Type	Percent of Microsite Types used by Fishers at Rest and Den Structures by Tree Species					
	California Black Oak (<i>n</i> = 387)	Canyon Live Oak (<i>n</i> = 15)	Incense Cedar (<i>n</i> = 131)	Ponderosa Pine (<i>n</i> = 165)	Sugar Pine (<i>n</i> = 55)	White Fir (<i>n</i> = 277)
Cavity						
Tree Cavity	91.7% (355)	66.7% (10)	50.4% (66)	18.2% (30)	29.1% (16)	52.3% (145)
Log Cavity	1.8% (7)	0.0% (0)	23.7% (31)	6.7% (11)	7.3% (4)	4.3% (12)
Platform - Branch						
Large Branch	3.6% (14)	0.0% (0)	7.6% (10)	4.8% (8)	9.1% (5)	3.3% (9)
Branch cluster	0.3% (1)	0.0% (0)	4.6% (6)	28.5% (47)	18.2% (10)	9.0% (25)
Mistletoe	0.0% (0)	6.7% (1)	0.0% (0)	4.8% (8)	7.3% (4)	2.2% (6)
Stick nest	0.0% (0)	20.0% (3)	4.6% (6)	22.4% (37)	20.0% (11)	5.1% (14)
Mixture of types listed above	0.0% (0)	0.0% (0)	2.3% (3)	7.9% (13)	1.8% (1)	2.9% (8)
Platform – Broken Top	2.6% (10)	6.7% (1)	6.9% (9)	6.7% (11)	7.3% (4)	20.9% (58)

Table 4. Habitat attributes measured at structure and site spatial scales to assess selection by female fishers at reproductive dens. We compared measurements collected at natal and maternal dens, then combined all dens to compare with available habitat in the same forest stand. Variables presented were included in habitat selection models, with the exception of distal canopy cover.

Habitat characteristics	Reproductive Dens (mean \pm SD)		Dens and Random Locations (mean \pm SD)	
	Natal ($n = 43$)	Maternal ($n = 96$)	Combined Dens ($n = 139$)	Random ($n = 139$)
Structure				
Percent hardwoods (vs conifers)	46.5%	53.1%	51.1%	43.9%
Percent live (vs dead)	79.1%	70.8%	73.4%	80.6%
Percent California black oak	46.5%	53.1%	51.1%	40.3%
Percent white fir	27.9%	22.9%	24.5%	18.7%
Percent incense cedar	16.3%	16.7%	16.5%	16.5%
Percent pine species	9.3%	7.3%	7.9%	20.9%
Percent other tree species	0.0%	0.0%	0.0%	3.6%
dbh – all trees (cm)	94.3 \pm 31.8	89.3 \pm 26.8	90.9 \pm 28.4	88.5 \pm 31.1
dbh – hardwood (cm)	76.9 \pm 22.2	74.3 \pm 17.5	75.1 \pm 18.8	64.0 \pm 18.9
dbh – conifer (cm)	109.5 \pm 31.5	105.7 \pm 25.7	106.9 \pm 27.6	107.6 \pm 24.8
Height – all trees (m)	27.7 \pm 12.7	22.9 \pm 11.8	24.4 \pm 12.2	28.6 \pm 14.9
Height – live hardwood (m)	19.8 \pm 5.9	17.7 \pm 6.1	18.3 \pm 6.1	18.2 \pm 6.4
Height – hardwood snag (m)	8.3 \pm 3.7	11.7 \pm 6.0	10.0 \pm 4.5	12.1 \pm 2.9
Height – live conifer (m)	38.7 \pm 9.2	37.1 \pm 9.2	37.8 \pm 9.1	42.8 \pm 9.8
Height – conifer snag (m)	28.6 \pm 12.9	21.7 \pm 12.7	23.3 \pm 12.9	24.2 \pm 14.8
Large Broken Limb	58.1%	53.1%	54.7%	39.6%
Site				
Proximal canopy cover 0-15m (%)	72.3 \pm 13.1	71.9 \pm 14.5	72.1 \pm 14.0	72.7 \pm 14.1
Distal canopy cover 20-30m (%)	68.7 \pm 17.8	68.5 \pm 14.7	---	---
Combined understory 0-3m (%)	55.3 \pm 24.0	56.9 \pm 21.4	56.4 \pm 22.2	56.6 \pm 22.5
Understory high 2-3m (%)	53.4 \pm 27.3	52.2 \pm 25.9	52.6 \pm 26.2	52.3 \pm 25.8
Understory low 1-2m (%)	52.9 \pm 27.8	53.8 \pm 23.3	53.5 \pm 24.7	53.3 \pm 24.7
Understory ground 0-1m (%)	59.6 \pm 22.4	64.8 \pm 21.8	63.2 \pm 22.0	64.2 \pm 2.5
Elevation (m)	1558 \pm 237	1518 \pm 24	1530 \pm 234	1529 \pm 20
Slope (%)	33.1 \pm 16.7	35.8 \pm 15.5	34.9 \pm 15.8	36.9 \pm 17.3
Aspect - northness	-0.034 \pm 0.737	-0.092 \pm 0.660	-0.074 \pm 0.683	-0.081 \pm 0.680
Aspect - eastness	-0.012 \pm 0.681	0.086 \pm 0.748	0.021 \pm 0.732	0.023 \pm 0.734

Table 5. Forest stand variables measured at stands used by fishers for reproductive dens. We present data for natal and maternal dens separately as well a combined for comparison with random forest stands within the collective home ranges of adult female fishers. Tree measurements were collected using the Common Stand Exam protocol and variables were calculated using the Suppose interface with the Forest Vegetation Simulator (FVS). We retained English units used in the Forest Vegetation Simulator program, but provide the conversions in a footnote. Trees per acre (TPA) were calculated for live California black oaks ($\geq 20''$ and $\geq 24''$) and all large live trees ($\geq 35''$). Stand density index reflects the number of trees per acre relative to the expected quadratic mean dbh by tree species (Husch et al. 2003).

Variable Description	Code Used in Model	Reproductive Den Stands (mean \pm SD)		Den and Random Stands (mean \pm SD)	
		Natal (<i>n</i> = 48)	Maternal (<i>n</i> = 95)	Dens Combined (<i>n</i> = 143)	Random (<i>n</i> = 145)
Variables Calculated in FVS					
Canopy cover	CC	76.4 \pm 15.6	77.7 \pm 15.7	77.2 \pm 15.6	67.8 \pm 20.2
CA black oak $\geq 20^1$ in dbh trees/acre	TPA (BO $\geq 20''$)	3.5 \pm 4.0	3.8 \pm 5.5	3.6 \pm 5.1	2.2 \pm 6.0
CA black oak ≥ 24 in dbh trees/acre	TPA (BO $\geq 24''$)	1.8 \pm 2.7	2.1 \pm 2.5	2.0 \pm 2.6	0.7 \pm 2.1
Basal area of CA black oak	BA (all BO)	24.5 \pm 28.3	25.5 \pm 23.5	25.2 \pm 25.2	16.0 \pm 28.2
Basal area of snags ≥ 30 in dbh	BA (snag $\geq 30''$)	17.5 \pm 23.9	15.8 \pm 18.9	16.3 \pm 20.7	9.4 \pm 23.3
Basal area of snags ≥ 35 in dbh	BA (snag $\geq 35''$)	13.9 \pm 23.0	13.3 \pm 17.4	13.5 \pm 19.3	5.7 \pm 20.2
Basal area of all live trees	BA (all)	221.0 \pm 69.8	224.6 \pm 78.7	223.4 \pm 75.6	209.6 \pm 100.2
Live trees ≥ 35 in dbh trees/acre	TPA ($\geq 35''$)	5.2 \pm 3.4	4.7 \pm 3.7	4.9 \pm 3.6	5.0 \pm 6.1
Stand density index	SDI	479.9 \pm 138.8	489.7 \pm 160.4	486.4 \pm 153.1	335.5 \pm 150.1
Tree height (ft)	tree ht	88.4 \pm 17.9	88.4 \pm 17.2	88.4 \pm 17.4	84.9 \pm 23.7
Variables Calculated in GIS					
Elevation (m)	elevation	1535.9 \pm 226.3	1486.6 \pm 216.4	1503.2 \pm 220.2	1556.2 \pm 313.5
Slope (%)	slope	34.9 \pm 15.2	35.5 \pm 14.2	35.3 \pm 14.5	29.1 \pm 15.5
Northness	northness	0.022 \pm 0.762	0.024 \pm 0.675	0.024 \pm 0.703	-0.008 \pm 0.717
Eastness	eastness	-0.112 \pm 0.654	-0.026 \pm 0.744	-0.545 \pm 0.714	0.051 \pm 0.700

¹ Conversions: 20 in = 51 cm, 24 in = 61 cm, 30 in = 76 cm, 35 in = 89 cm, 1 ft = 0.3 m, 1 acre = 0.4 ha.

Table 6. Logistic regression models used to compare characteristics of fisher denning habitat to available habitat. At the structure and site spatial scales, den locations were paired with random locations within the same forest stand. Live represents live trees (versus snags). Hardwood stands for hardwood tree species (versus conifers). CC 0-15m stands for proximal canopy cover 0-15 m from the den tree and elev represents elevation (meters). Further information on variables in the models are in Tables 4. K = number of model parameters. Models were ranked and listed by AICc values, Akaike weights (w_i), and percent AUC (area under the curve). Parameter coefficients for top ranked model(s) are shown in Table 8.

Model	K	AICc	Δ AICc	w_i	AUC (%)
Structure					
Dbh + decay + black oak + white fir + incense cedar + large broken limb	6	363.5	0.0	0.674	69.9
Dbh + decay + black oak + white fir + broken limb	5	365.4	1.9	0.261	69.2
Height + decay + black oak + white fir + incense cedar + large broken limb	6	369.0	5.5	0.043	68.4
Dbh + decay + black oak	3	371.1	7.6	0.015	65.8
Dbh + black oak + white fir + incense cedar + large broken limb	5	372.5	9.0	0.007	67.7
Height + live + hardwood	3	385.9	22.4	0.000	58.9
Site					
CC 0-15m + understory 0-1m + elev + understory 0-1m*elev + slope	5	391.2	0.0	0.281	57.7
CC 0-15m + understory 0-1m + slope	3	392.2	1.0	0.170	53.5
CC 0-15m + understory 0-3m + slope	3	392.4	1.2	0.154	52.8
Understory 0-1m + elev + understory 0-3*elevation	3	392.6	1.4	0.140	52.4
Elevation + slope + northness + eastness	4	394.5	3.3	0.054	52.0
CC 0-15m + slope + northness + eastness	4	394.5	3.3	0.054	52.5
CC 0-15m + understory 0-3m + elev + slope	4	394.5	3.3	0.054	53.0
Understory 0-3m + slope + northness + eastness	4	394.6	3.4	0.051	52.8
CC 0-15m + understory 0-1m + elev + understory 0-1m*elev + slope + northness + eastness	7	395.4	4.2	0.034	57.8
CC 0-15m + understory 0-3m + elev + slope + northness + eastness	6	398.6	7.4	0.007	52.9

Table 7. Coefficients and associated statistics for the top models described in Tables 6 and 7. Codes for stand level coefficients can be found in Table 5.

Model	Coefficient	Estimate	SE	Z	CI
Structure					
	Intercept	-3.574	0.802	-4.458	-5.221, -2.067
	Dbh cm	0.014	0.006	2.391	0.003, 0.025
	Decay	0.275	0.086	3.212	0.111, 0.449
	Black oak (yes)	1.930	0.492	3.921	1.004, 2.943
	White fir (yes)	1.468	0.462	3.179	0.586, 2.406
	Incense cedar (yes)	0.940	0.478	1.966	0.017, 1.901
	Large broken limb (yes)	0.514	0.275	1.873	-0.023, 1.056
Site					
	Intercept	6.642	3.001	2.213	0.890, 12.720
	Proximal canopy cover 0-15m	-0.005	0.009	-0.591	-0.023, 0.012
	Understory 0-1m	-0.092	0.041	-2.249	-0.174, -0.014
	Elevation	-0.004	0.002	-2.073	-0.007, -0.0003
	Slope	-0.008	0.008	-1.024	-0.023, 0.007
	Understory 0-1m*Elevation	0.00006	0.00003	2.213	0.000008, 0.0001
Stand					
	Intercept	1.067	1.219	0.876	-1.352, 3.455
	Canopy cover	-0.049	0.013	-3.685	-0.075, -0.024
	TPA (BO $\geq 24''$)	0.263	0.082	3.224	0.112, 0.432
	BA (snag $\geq 35''$)	0.011	0.009	1.259	-0.005, 0.030
	SDI	0.012	0.002	6.509	0.008, 0.015
	Elevation	-0.003	0.001	-3.850	-0.004, -0.001
	Slope	0.041	0.011	3.877	0.021, 0.062

Table 8. Logistic regression models used to compare characteristics of fisher denning habitat to available habitat. At the forest stand spatial scale, stands containing fisher dens were compared with random stands within the combined home ranges of adult female fishers in the study area. Further information on variables in the models are in Table 5. K = number of model parameters. Models were ranked and listed by AICc values, Akaike weights (w_i), and percent AUC (area under the curve). Parameter coefficients for top ranked model(s) are shown in Table 8.

Stand Model	K	AICc	Δ AICc	w_i	AUC (%)
CC + TPA (BO \geq 24") + BA (snag \geq 35") + SDI + elevation + slope	6	294.7	0.0	0.998	85.2
CC + TPA (BO \geq 24") + BA (snag \geq 35") + SDI + slope	5	308.8	14.1	0.001	83.5
CC + TPA (BO \geq 24") + BA (snag \geq 35") + SDI + elevation	5	309.2	14.5	0.001	82.9
SDI + tree height + elevation + slope + northness + eastness	6	318.9	24.2	0.000	81.8
CC + TPA (BO \geq 24") + BA (snag \geq 35") + SDI	4	320.7	26.0	0.000	81.4
CC + TPA (BO \geq 24") + BA (snag \geq 35") + elevation + slope	5	354.3	59.6	0.000	77.7
CC + TPA (BO \geq 24") + BA (snag \geq 35") + BA (all) + elevation + slope	6	355.5	60.8	0.000	77.5
CC + TPA (BO \geq 24") + BA (snag \geq 35")	3	357.7	63.0	0.000	76.1
CC + TPA (BO \geq 24") + BA (snag \geq 35") + elevation + slope + northness + eastness	7	358.2	63.5	0.000	77.8
TPA (BO \geq 24") + BA (snag \geq 35") + TPA (\geq 35")	3	365.9	71.2	0.000	77.2
CC + BA (snag \geq 35") + BA (all)	3	370.7	76.0	0.000	72.1
CC + BA (BO) + BA (snag \geq 35") + elevation + slope + northness + eastness	7	372.4	77.7	0.000	73.9
CC + TPA (BO \geq 24") + BA (all)	3	374.7	80.0	0.000	69.2
CC + TPA (BO \geq 20") + BA (snag \geq 30") + elevation + slope + northness + eastness	7	375.8	81.1	0.000	72.3
BA (all) + tree height + elevation + slope + northness + eastness	6	391.3	96.6	0.000	65.4

Figure 1. Numerous factors may influence habitat selection by female fishers during the reproductive period. Characteristics of habitat at different spatial scales may play a role in the den selection process. Additionally, abiotic factors (e.g., distance to a water source, temperature) or biotic factors (e.g., proximity to conspecifics, prey, competitors, predators) may affect suitability of a location. Below we present some of the potential factors that may affect suitability of a location at the spatial scales referenced in our study. Photos exemplify representative reproductive dens in the southern Sierra Nevada: a) female fisher carrying kit down trunk of natal den, b) entrance to a natal den in a hardwood snag (30 cm rule for scale), c) interior of a natal den microsite in a live hardwood with a resting kit (photo taken from camera inserted in the den entrance and oriented vertically down), d) female climbing a conifer snag to a natal den microsite entrance, and e) female at a maternal den microsite entrance in a hardwood.

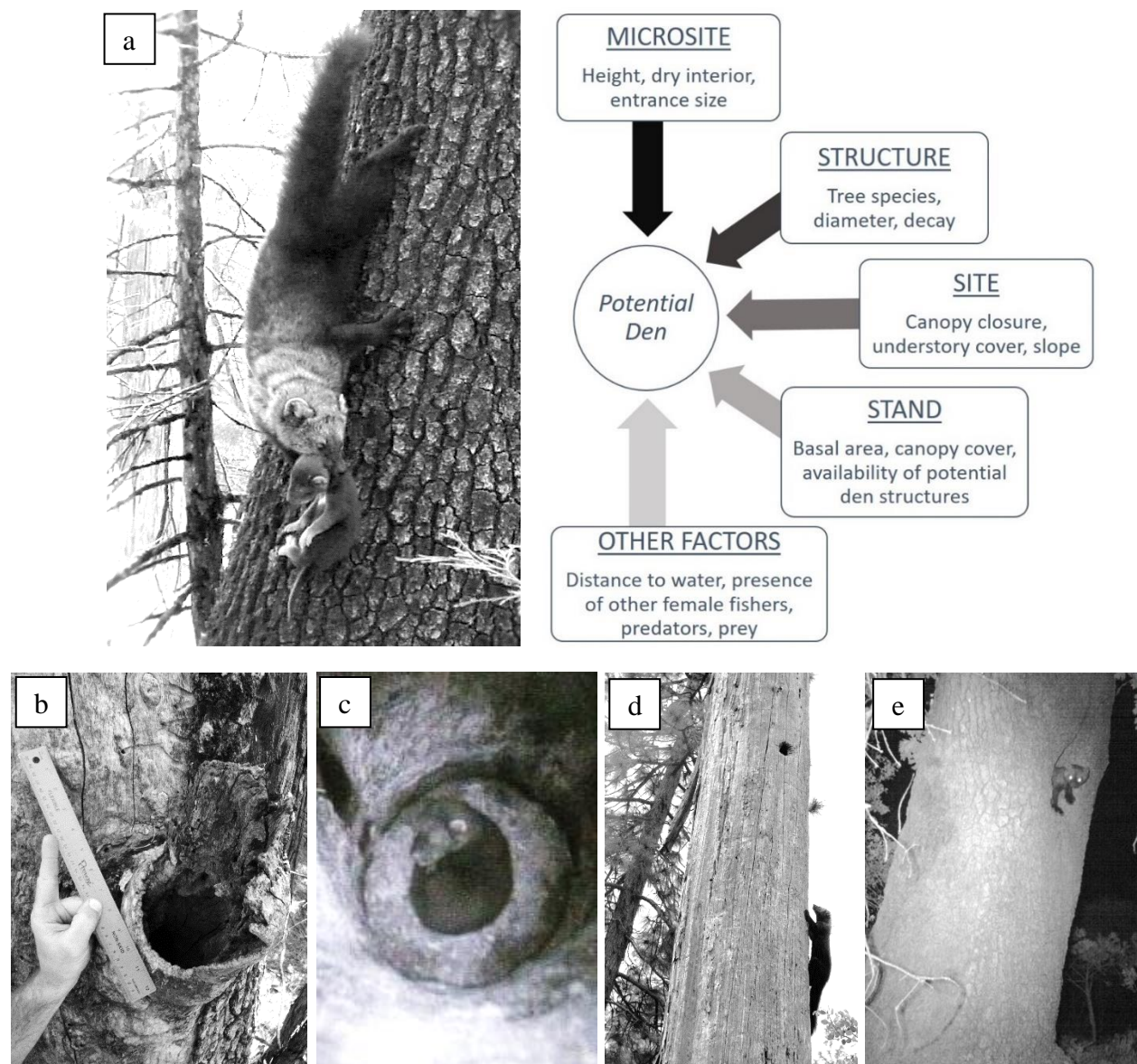


Figure 2. Location of the Kings River study area (a) in the southwestern portion of the Sierra National Forest in the southern Sierra Nevada. (b) Combined home range area of all reproductive females over the course of the study (2007-2015).

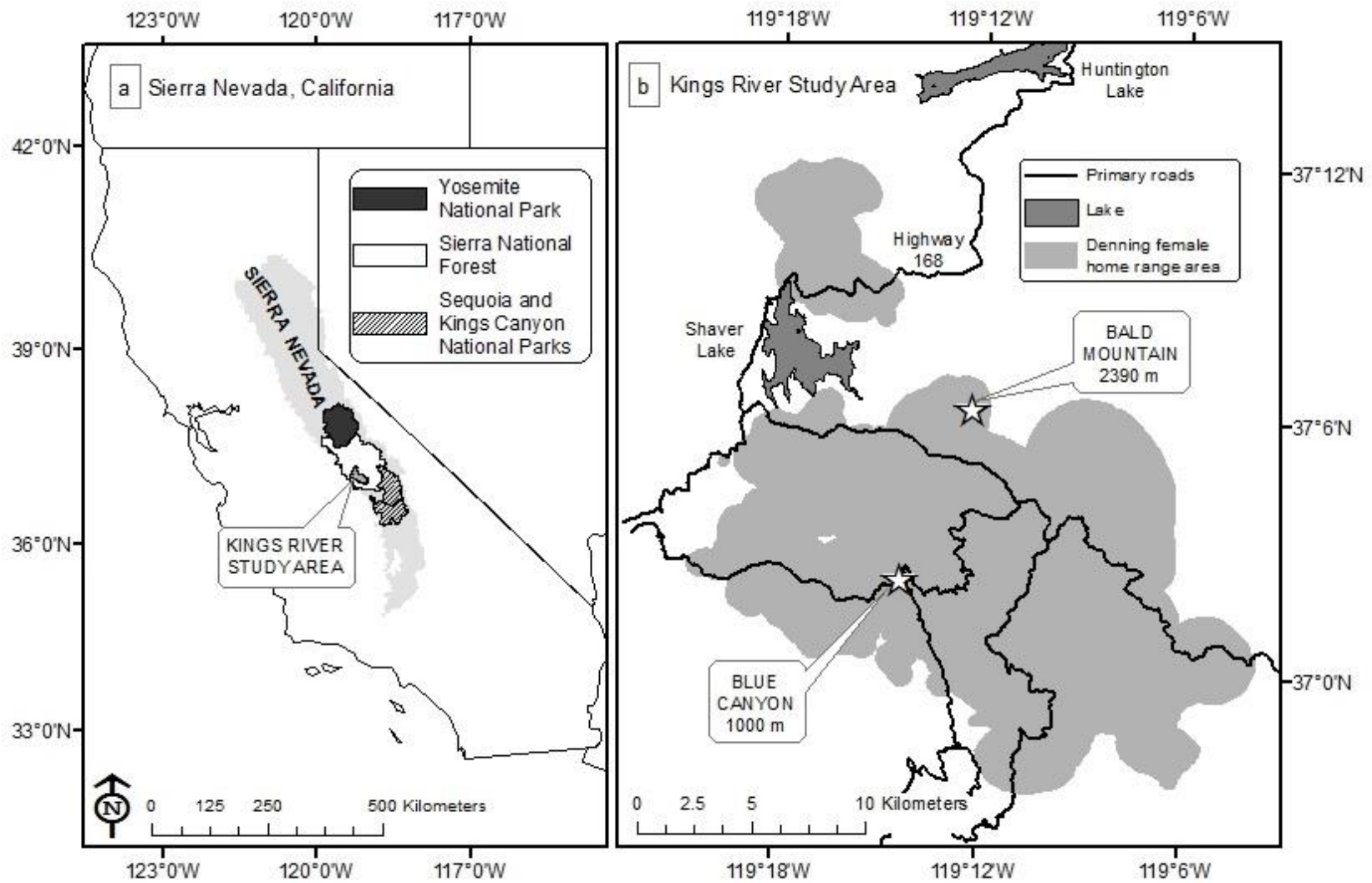


Figure 3. Vegetation sampling designs used at fisher reproductive dens and random locations. (a) Canopy cover was measured with a moosehorn at 14 proximal (solid circles) and 12 distal (empty circles) points on 2 perpendicular transects centered on den and paired random trees. Understory cover was assessed with a 3 x 0.5 m cover cloth marked with 10 x 10 cm squares in 3 sections: ground (0-1m), low (1-2m), and high (2-3m); the cloth was held at 10 m from center (rectangles) and read by a person at the center. Panel (b) shows the layout of 5 Common Stand Exam (CSE) plots clustered at a den tree (left) and dimensions of an individual CSE plot (right).

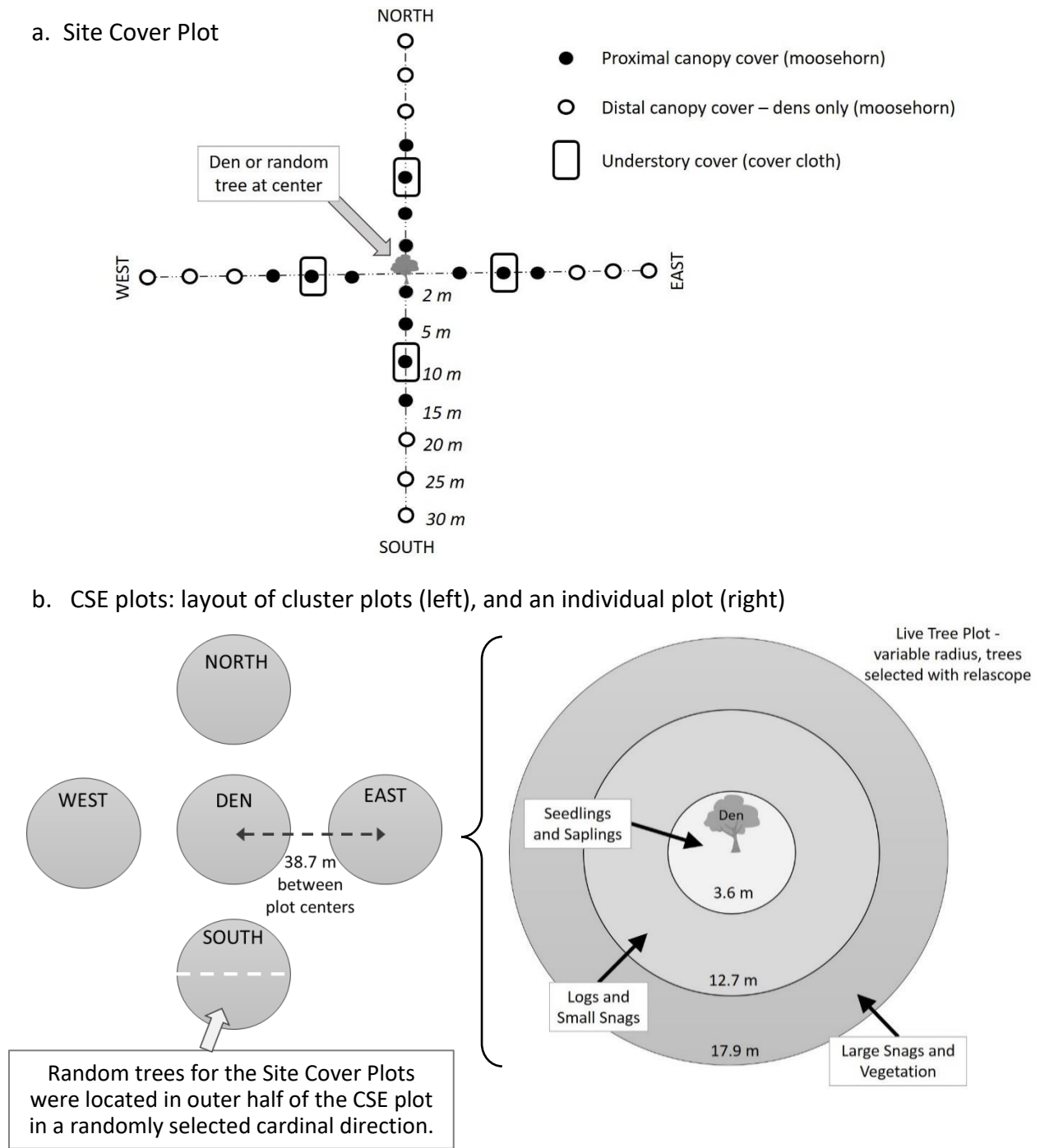


Figure 4. Proportion of microsites used by fishers in the southern Sierra Nevada. Microsites were classified into 6 categories and separated here by use for resting (males, females, combined) or denning (natal, maternal, combined). Branch type platforms include branch clusters, large branches, nests, and/or mistletoe. Broken top platforms denote features where the main trunk of the tree has broken, creating a platform; these types of platform are most common in snags and are often open to the sky. Burrows include holes in the ground, rock piles, stumps, and/or snow. Interstitial spaces include large slash piles, spaces under suspended logs, and within culverts. All microsites that could be identified in a structure with a high level of certainty are represented; microsites used on > 1 occasion were counted only once per category.

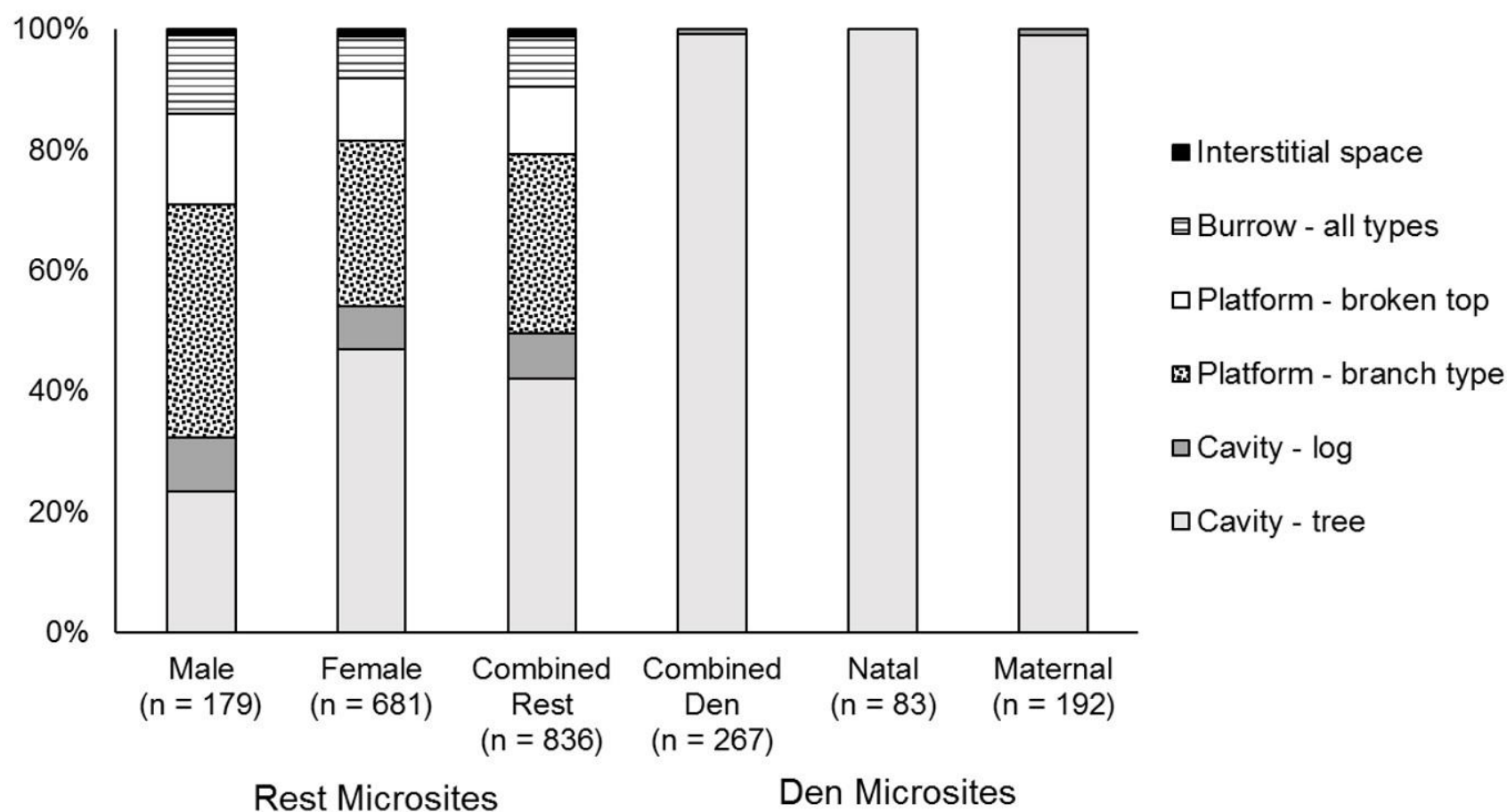


Figure 5. Types of structures used by fishers (sexes combined) for resting (left, a – c) relative to those selected by females for natal and maternal dens (right, d – f). Log includes hardwood and conifer species, and Other includes ground-level structures such as rock piles, ground burrows, snow burrows, or slash piles. Structures used on > 1 occasion were counted once per category.

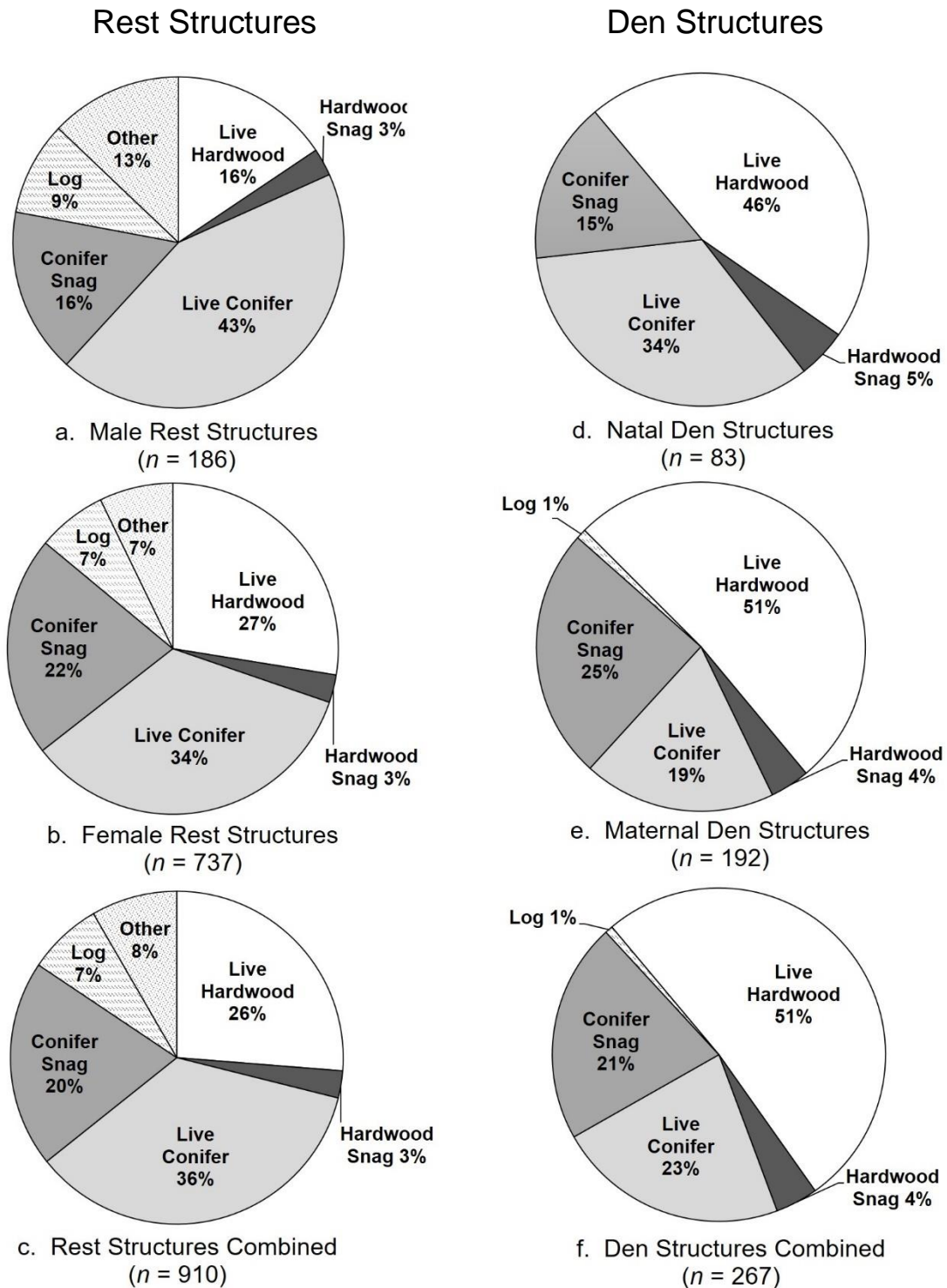


Figure 6. Summary of fisher use of structures (live tree, snag, log) by tree species in the southern Sierra Nevada for resting and denning. The upper graph (a) compares structures used by male and female fishers for resting with those used by reproductive females for natal and maternal dens. The lower graph (b) compares all rest structures (male and female combined) with all den structures (natal and maternal combined). Structures used on > 1 occasion by a fisher were counted only once per category.

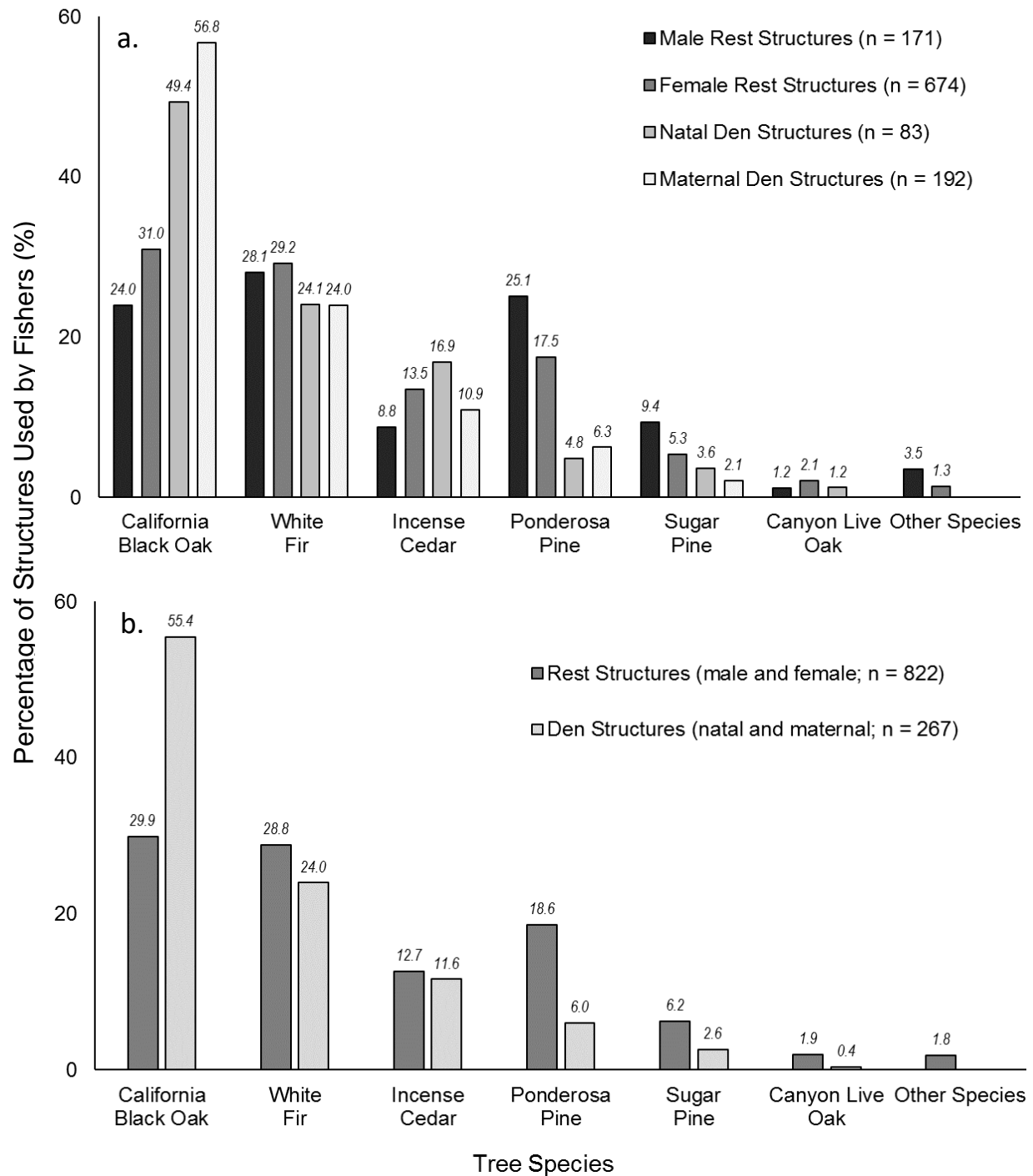


Figure 7. Box plots displaying heights of microsites used by fishers for reproduction. In panel (a), early dens (natal and maternal dens located in March and April) generally were higher than later dens (maternal dens located in May and June). Panel (b) shows the height of microsites at natal (left) and maternal (right) dens relative to structure type, with CN denoting conifer and HW denoting hardwood trees. Boxes represent the 25th and 75th percentiles, horizontal lines represent median values, whisker bars denote standard error, and outliers are shown with black dots. Panel (a) includes outliers only within the 5 to 95 percentile range while (b) includes all outliers. Microsites used on > 1 occasion by a fisher were counted only once per category

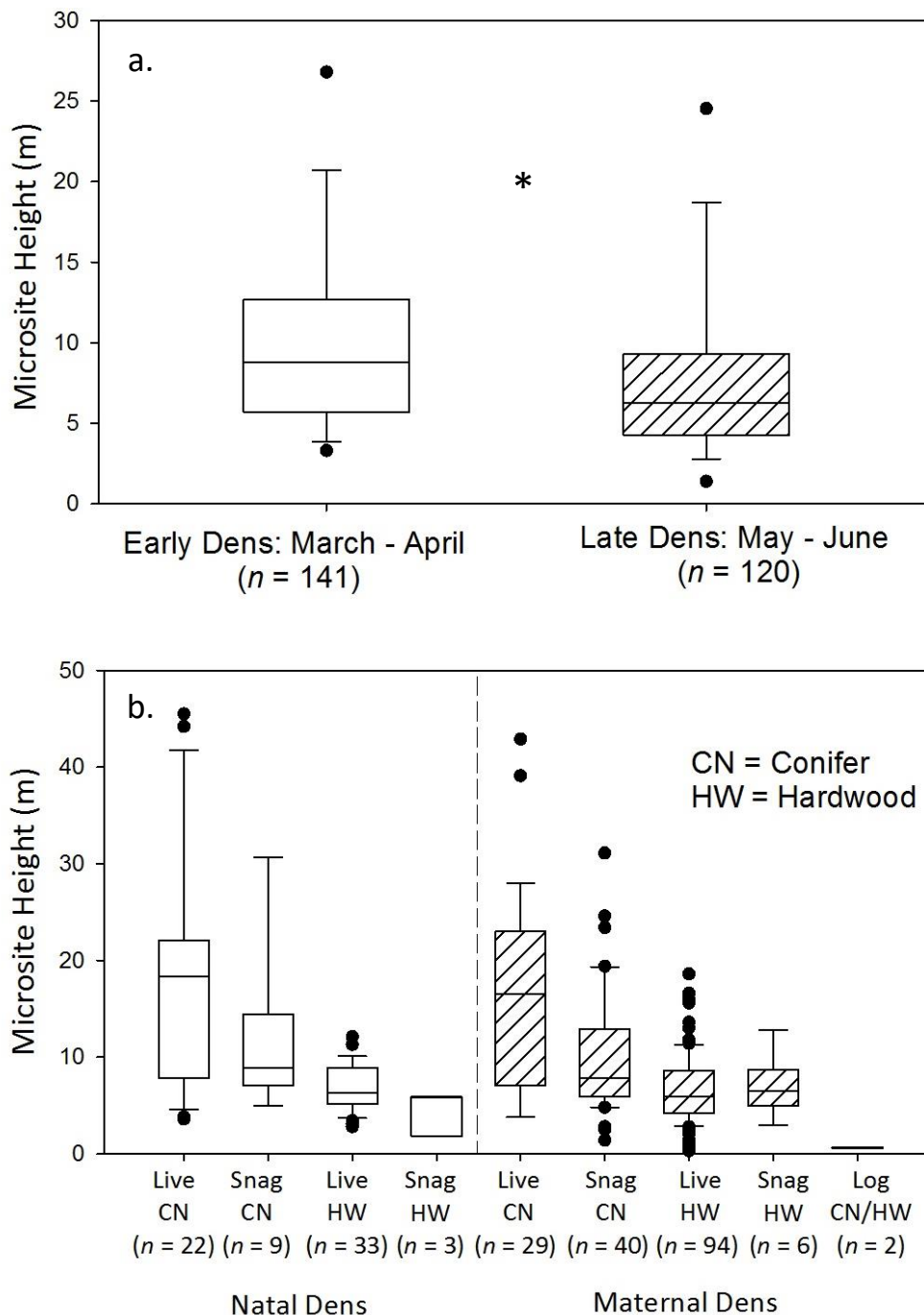


Figure 8. Diameter at breast height (dbh) of trees used as rest structures by male and female fishers and as reproductive den structures by females. Plots are grouped by conifers on the left [(a) live, (b) snags/logs] and hardwoods on the right [(c) live, (d) snags/logs]. Note that 1 outlier, a giant sequoia log (dbh = 323 cm) used as a male rest sites is not shown. Structures used on > 1 occasion by a fisher were counted only once per category. Asterisks indicate statistical differences between (panel a) live conifers used for resting (sexes combined) versus denning (natal and maternal dens combined) and (panel b) conifer snags used for resting by males versus females. Symbols as in Fig. 7.

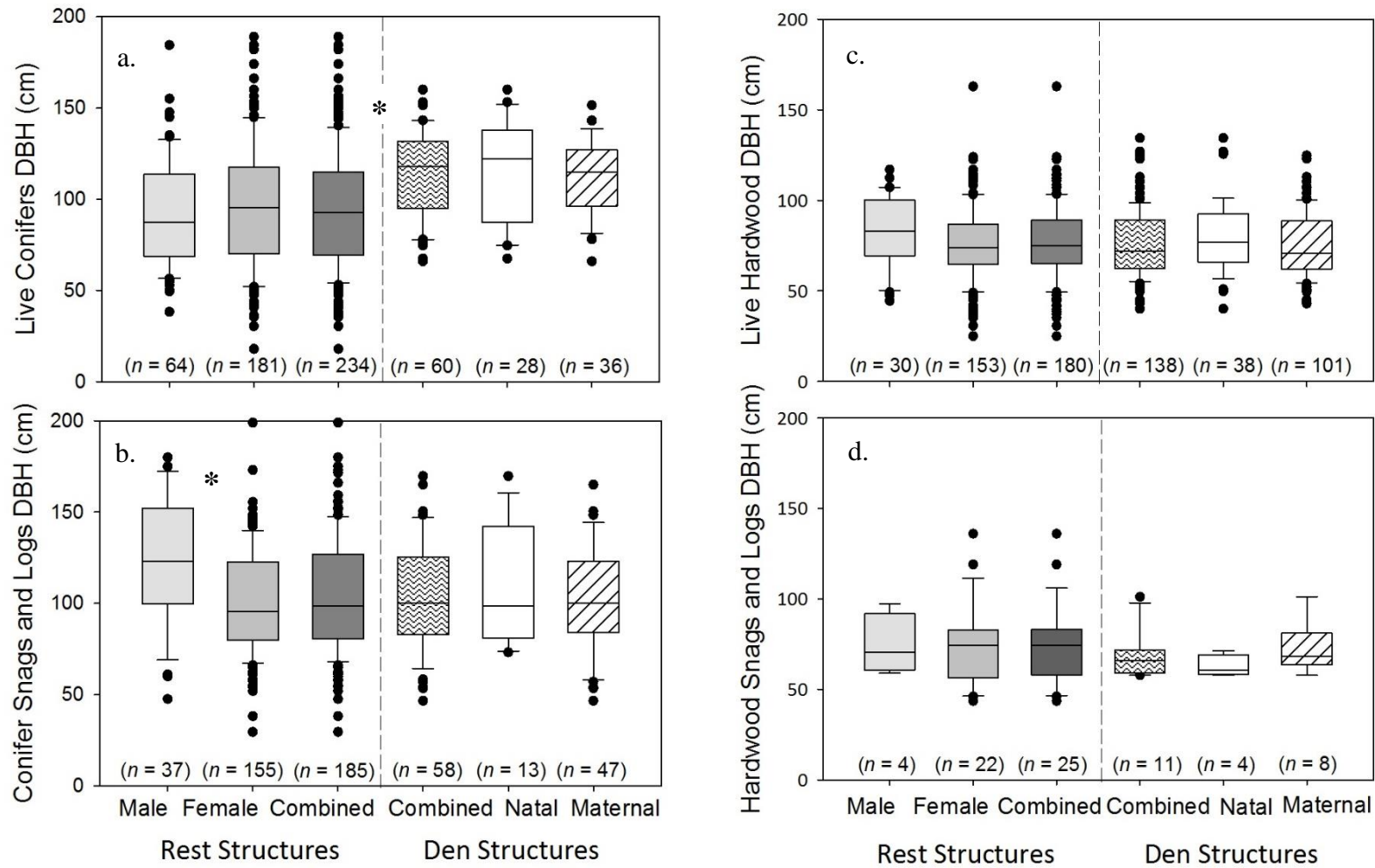
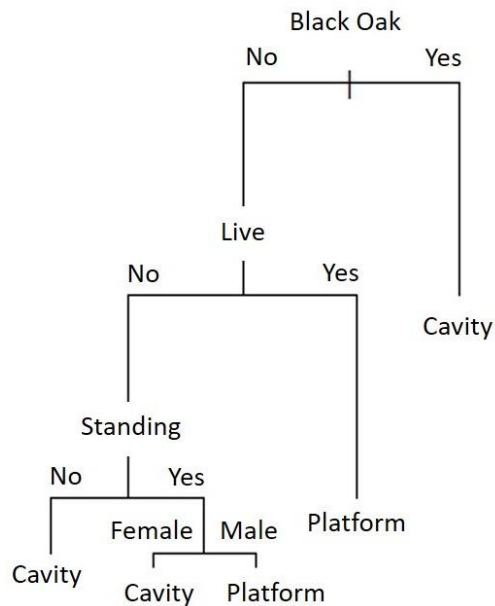
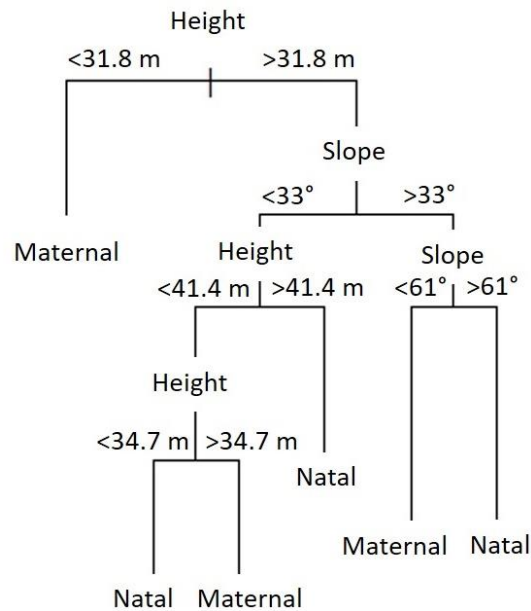


Figure 9. Classification trees highlighting characteristics of structures (live trees, snags, or logs) with cavity microsites that were used by fishers. Trees were pruned to balance misclassification, deviance, and interpretability. Tree (a) predicts use of cavity vs. platform microsites used as fisher rest structures. Tree (b) shows the most relevant variables associated with distinguishing natal and maternal den structures. Tree (c) depicts the most relevant variables associated with cavity or platform microsites for structures used by fishers for both resting and denning.

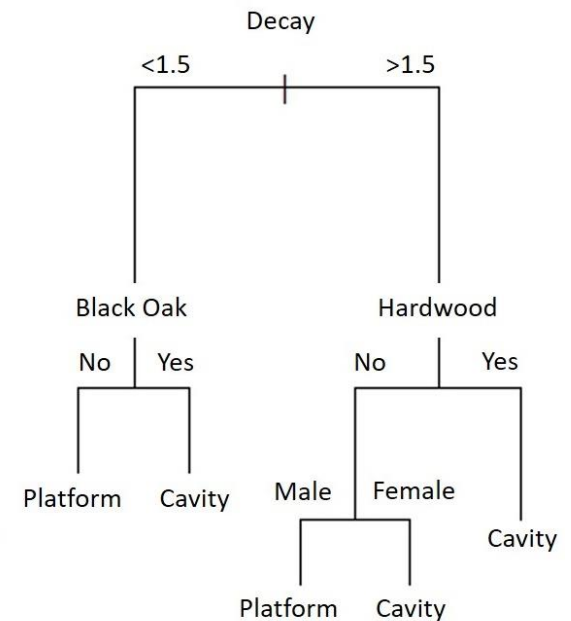
a. Male and Female Rest Structures
(misclassification rate = 18.1%)



b. Den Structures
(misclassification rate = 23.5%)



c. Den and Rest Structures
(misclassification rate = 14.9%)



Appendix A. Examples of microsites used by fishers in the southern Sierra Nevada. Male and female fishers used branch platforms such as (a) large branches, (b) branch clusters (brooms), (c) broken tops, and (d) cavities in logs for resting. Reproductive female fisher used tree cavities accessed through (e) broken limbs (fisher head visible in cavity entrance), (f) pileated woodpecker (*Dryocopus pileatus*) holes, and (g) other openings resulting from scars. Kits were kept and cared for in (h) cavity chambers within the bores of trees.

a.



e.



b.



f.



c.



g.



d.



h.



Appendix B. Distribution of microsite and structure types used for resting (male, female, sexes combined) and denning (natal den, maternal den, dens combined) by fishers in the Kings River study area from 2007 to 2015. Microsites or structures used on > 1 occasion by a fisher were counted only once per category, although the total number of uses recorded and percent reuse are shown.

Microsite and Structure Types	% of All Uses by Resting Fishers (<i>n</i> = unique microsites or structures)			% of All Uses by Denning Fishers (<i>n</i> = unique microsites or structures)		
	Male	Female	Sexes Combined	Natal	Maternal	Dens Combined
Microsites						
Cavity – Tree	23.5% (42)	47.0% (320)	42.1% (352)	100.0% (83)	99.0% (190)	99.3% (265)
Cavity – Log	8.9% (16)	7.0% (48)	7.5% (63)	---	1.0% (2)	0.7 % (2)
Platform – Branch type	38.5% (69)	27.5% (187)	29.7% (248)	---	---	---
Platform – Broken top	15.1% (27)	10.3% (70)	11.1% (93)	---	---	---
Burrow	12.8% (23)	7.0% (48)	8.4% (70)	---	---	---
Interstitial space	1.1% (2)	1.2% (8)	1.2% (10)	---	---	---
Unique microsites	179	681	836	83	192	267
All documented uses	199	763	962	95	206	301
% Reuse	10.1%	10.7%	8.5%	12.6%	14.0%	11.3%
Structures						
Hardwood – Live	15.6% (39)	27.5% (203)	26.3% (239)	45.8% (38)	55.2% (101)	51.3% (137)
Hardwood – Snag	2.7% (5)	2.7% (20)	2.6% (24)	4.8% (4)	4.2% (7)	4.1% (11)
Conifer – Live	43.5% (81)	34.2% (252)	35.4% (322)	33.7% (28)	20.3% (36)	22.5% (60)
Conifer – Snag	16.1% (30)	21.6% (159)	20.1% (183)	15.7% (13)	26.6% (46)	21.3% (57)
Log	9.1% (17)	6.8% (50)	7.3% (66)	---	1.0% (2)	0.7% (2)
Other	12.9% (24)	7.2% (53)	8.4% (76)	---	---	---
Unique structures	196	737	910	83	192	267*
All documented uses	216	824	1040	95	206	301
% Reuse	9.3%	10.4%	12.5%	12.6%	14.0%	11.3%

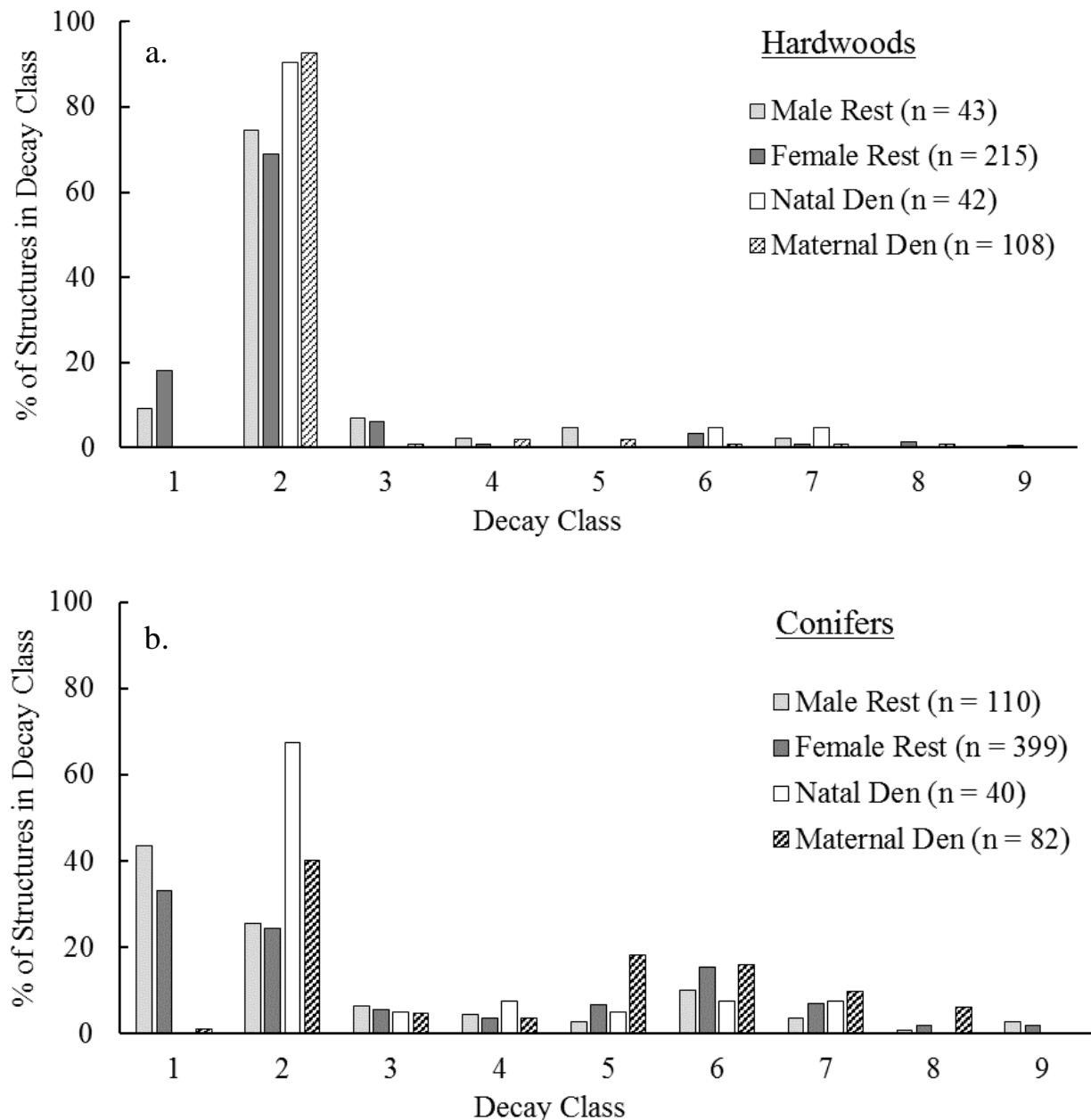
Appendix C. Summary of the types of microsites used by male and female fishers for resting throughout the year compared to those used by females during reproduction at natal dens and maternal dens on the Sierra National Forest from June 2007 through 2015. For microsites used on >1 occasion, each instance was included to reflect frequency of use. Dashes indicate cells that were not observed.

Microsite Type	Resting Microsites % (<i>n</i>)		
	Male (<i>n</i> = 199)	Female (<i>n</i> = 763)	Combined (<i>n</i> = 962)
Cavity – Tree (live or snag)	25.6% (51)	48.0% (366)	43.3% (417)
Cavity – Log	8.5% (17)	6.7% (51)	7.1% (68)
Platform - Branch			
Branch cluster	13.1% (26)	10.1% (77)	10.7% (103)
Nest or nest-like feature	10.1% (20)	7.5% (57)	8.0% (77)
Large branch	10.1% (20)	4.1% (31)	5.3 % (51)
Mistletoe	---	1.8% (14)	1.5% (14)
Combination of above	5.0% (10)	3.3% (25)	3.6% (35)
Platform – Broken Top	14.1% (28)	10.7% (82)	11.4% (110)
Burrow			
Ground	1.0% (2)	1.6% (12)	1.5% (14)
Rocks	9.5% (19)	3.7% (28)	4.9 % (47)
Stump	1.0% (2)	1.0% (8)	1.0% (10)
Snow	1.0% (2)	0.3% (2)	0.4% (4)
Interstitial Space			
Space under log or log pile (natural)	0.5% (1)	0.5% (4)	0.5% (5)
Large slash pile (human created)	---	0.8% (6)	0.6% (6)
Culvert	0.5% (1)	---	0.1% (1)

Appendix D. Characteristics of fisher habitat use at microsites and structures used for resting by male and female fishers on the Sierra National Forest between 2007 and 2015. Tree measurements were subdivided into hardwood and conifer species, and live or dead structures, due to potential differences between these categories. See Appendix F and G for diameters of individual tree species. Microsites or structures used on > 1 occasion by a fisher were counted only once per category. We used a Bonferroni-adjusted *P* value of 0.003 for significance, reflecting an alpha value of 0.05 and 18 tests; bold letters denote statistical differences.

Habitat Characteristics	Rest Microsites and Structures		
	Mean \pm SD (<i>n</i>)		
	Male	Female	Sexes Combined
Microsite Height (m)			
All (tree, ground)	8.8 \pm 7.6 (104)	8.9 \pm 8.0 (354)	8.8 \pm 7.8 (443)
Hardwood – Live	7.3 \pm 4.4 (23)	7.1 \pm 5.7 (111)	7.1 \pm 5.5 (131)
Hardwood – Snag	6.3 \pm 4.2 (4)	5.4 \pm 1.8 (12)	5.6 \pm 2.5 (15)
Conifers – Live	16.2 \pm 6.2 (33)	17.1 \pm 7.2 (90)	16.7 \pm 6.9 (116)
Conifer – Snag	10.4 \pm 4.9 (18)	10.3 \pm 5.7 (72)	10.4 \pm 5.5 (88)
Structure Height (m)			
Hardwood – Live	21.2 \pm 9.4 (28)	20.4 \pm 7.8 (136)	20.4 \pm 8.0 (161)
Hardwood – Snag	11.4 \pm 7.1 (4)	10.9 \pm 4.5 (16)	11.2 \pm 4.9 (19)
Conifer – Live	36.1 \pm 9.8 (62)	39.0 \pm 11.7 (160)	38.2 \pm 11.2 (211)
Conifer – Snag	15.4 \pm 10.6 (22)	16.8 \pm 10.4 (103)	16.7 \pm 10.6 (121)
Structure dbh (cm)			
Hardwood – All			76.4 \pm 20.6 (205)
Hardwood – Live	83.0 \pm 19.5 (30)	75.8 \pm 20.6 (153)	76.6 \pm 20.5 (180)
Hardwood – Snag/Log	74.3 \pm 16.8 (4)	73.7 \pm 22.7 (22)	74.4 \pm 21.8 (25)
Conifer All			99.6 \pm 34.5 (418)
Conifer – Live	92.6 \pm 30.3 (64)	95.8 \pm 34.5 (181)	94.9 \pm 33.6 (234)
Conifer – Snag/Log	127.2 \pm 47.4 (37)	100.3 \pm 28.5 (154)	105.5 \pm 34.8 (185)
Topography at Structure			
Elevation (m a.s.l.)	1602 \pm 302 (191)	1524 \pm 232 (731)	1541 \pm 250 (898)
Slope (%)	32.6 \pm 17.1 (143)	32.0 \pm 17.7 (495)	32.0 \pm 17.6 (616)
Aspect (degrees)	186 \pm 92 (157)	190 \pm 98 (522)	188 \pm 96 (657)

Appendix E. Distribution of decay classes (Maser et al. 1979) for live trees and snags (combined) used as fisher rest structures and den structures. Decay class 1 represents live healthy trees and class 2 denotes live but declining trees. Decay class 3 represents recently dead trees while classes 4 and above correspond with increasing levels of decomposition and loss of height. Hardwoods (a) and conifers (b) are segregated due to potential differences in patterns of decay. Structures used on > 1 occasion by a fisher were counted only once per category.



Appendix F. Diameter at breast height (dbh) in metric units (cm) for trees used as rest (sexes combined) and den structures (natal and maternal combined) by fishers in the southern Sierra Nevada. Codes: M = male, F = female, ND = natal den, MD = maternal den.

Tree Species	Rest Structure dbh (cm) – Sexes Combined			Den Structure dbh (cm) – Dens Combined		
	Mean \pm SD (range)	M (n)	F (n)	Mean \pm SD (range)	ND (n)	MD (n)
Live Tree						
Hardwood						
Big leaf maple	43.0 \pm 8.5 (37.0 – 49.0)	0	2			
California black oak	78.7 \pm 19.5 (35.2 – 163.0)	28	140	76.0 \pm 18.5 (40.1 – 134.5)	37	101
Canyon live oak	58.2 \pm 24.8 (25.0 – 97.0)	1	6	98.0 (0)	1	0
White alder	59.1 \pm 22.3 (38.5 – 87.5)	1	3			
Conifer						
Incense cedar	116.3 \pm 39.8 (42.0 – 204)	8	29	124.3 \pm 21.7 (88.0 – 153.2)	10	9
Jeffrey pine	88.2 \pm 23.9 (66.0 – 113.5)	2	1			
Ponderosa pine	88.2 \pm 31.0 (36.5 – 184.5)	27	63	117.4 \pm 23.5 (74.9 – 139.8)	3	4
Sugar pine	104.0 \pm 34.4 (52.0 – 155.1)	7	15	123.0 \pm 13.8 (107.3 – 133.4)	1	2
White fir	90.7 \pm 28.9 (18.0 – 184.5)	17	69	105.7 \pm 23.5 (67.5 – 160.0)	14	20
Snags and Logs						
Hardwood						
California black oak	74.1 \pm 21.9 (43.5 – 136.0)	3	21	69.2 \pm 12.6 (57.8 – 101.1)	4	8
Canyon live oak	65.5 (0)	1	0			
Conifer						
Giant sequoia	323.0 (0)	1	0			
Incense cedar	98.0 \pm 33.6 (29.5 – 199.0)	5	34	102.8 \pm 23.0 (73.1 – 148.5)	4	12
Jeffrey pine	138.8 (0)	0	1			
Ponderosa pine	99.4 \pm 26.4 (47.5 – 145.0)	5	20	96.5 \pm 29.0 (46.6 – 129.5)	1	8
Red fir	137.4 (0)	0	1			
Sugar pine	130.5 \pm 27.8 (89.0 – 180.0)	5	8	138.4 \pm 22.6 (72.2 – 169.7)	2	2
White fir	105.0 \pm 30.2 (55.0 – 171.7)	22	83	103.3 \pm 28.5 (53.5 – 150.4)	6	26

Appendix G. Diameter at breast height (dbh) in English units (in) for trees used as rest (sexes combined) and den structures (natal and maternal combined) by fishers in the southern Sierra Nevada. Codes: M = male, F = female, ND = natal den, MD = maternal den.

Tree Species	Rest Structure dbh (in) – Sexes Combined			Den Structure dbh (in) – Dens Combined		
	Mean \pm SD (range)	M (n)	F (n)	Mean \pm SD (range)	ND (n)	MD (n)
Live Tree						
Hardwood						
Big leaf maple	16.9 \pm 3.3 (14.6 – 19.3)	0	2			
California black oak	31.0 \pm 7.7 (13.9 – 64.2)	28	140	29.9 \pm 7.3 (15.8 – 53.0)	37	101
Canyon live oak	22.9 \pm 9.8 (9.9 – 38.2)	1	6	38.6 (0)	1	0
White alder	23.3 \pm 8.8 (15.2 – 34.5)	1	3			
Conifer						
Incense cedar	45.8 \pm 15.7 (16.5 – 80.4)	8	29	49.0 \pm 8.5 (34.7 – 60.4)	10	9
Jeffrey pine	34.8 \pm 9.4 (26.0 – 44.7)	2	1			
Ponderosa pine	34.8 \pm 12.2 (14.4 – 72.7)	27	63	46.3 \pm 9.3 (29.5 – 55.1)	3	4
Sugar pine	41.0 \pm 13.6 (20.5 – 61.1)	7	15	48.5 \pm 5.4 (42.3 – 52.6)	1	2
White fir	35.7 \pm 11.4 (7.1 – 72.7)	17	69	41.6 \pm 9.3 (26.6 – 63.0)	14	20
Snags and Logs						
Hardwood						
California black oak	29.2 \pm 8.6 (17.1 – 53.6)	3	21	27.3 \pm 5.0 (22.8 – 39.8)	4	8
Canyon live oak	25.8 (0)	1	0			
Conifer						
Giant sequoia	127.3 (0)	1	0			
Incense cedar	38.6 \pm 13.2 (11.6 – 78.4)	5	34	40.5 \pm 9.1 (28.8 – 58.5)	4	12
Jeffrey pine	54.7 (0)	0	1			
Ponderosa pine	39.2 \pm 10.4 (18.7 – 57.1)	5	20	38.0 \pm 11.4 (18.4 – 51.0)	1	8
Red fir	54.1 (0)	0	1			
Sugar pine	51.4 \pm 11.0 (35.1 – 70.9)	5	8	54.5 \pm 8.9 (28.4 – 66.9)	2	2
White fir	41.4 \pm 11.9 (21.7 – 67.6)	22	83	40.7 \pm 11.2 (21.1 – 59.3)	6	26

Appendix H. Summary of decay-related characteristics observed at a subset of natal and maternal fisher den structures ($n = 139$) and paired random trees ($n = 139$) located in the Sierra National Forest between 2008 and 2012. Each den tree contained at least 1 cavity in the bole of the tree which was used by a reproductive female to house her kits. Visual detection of known den cavities from the ground was variable; some cavities were readily seen with the naked eye, whereas others were located only after searching with binoculars; the most cryptic cavities were verified only using telemetry or climbing the den tree. Cavities in hardwoods (live or snags) and conifer snags generally were easier to see from the ground than cavities in live conifers. The number of cavities in random trees may underrepresent the total number in the tree.

Feature	% Den Structures with Feature	% Random Trees with Feature
Cavity in bole	100.0 ($n = 139$)	29.5 ($n = 41$)
Large broken limb	54.7 ($n = 76$)	39.6 ($n = 55$)
Large dead limb	51.1 ($n = 71$)	60.4 ($n = 84$)
Woodpecker activity	33.8 ($n = 47$)	18.7 ($n = 26$)
Broken top	30.9 ($n = 43$)	24.5 ($n = 34$)
Major scar	27.3 ($n = 38$)	22.3 ($n = 31$)
Large bulge	23.0 ($n = 32$)	10.8 ($n = 15$)
Basal hollow	22.3 ($n = 31$)	17.3 ($n = 24$)
Major fork broken	20.1 ($n = 28$)	11.5 ($n = 16$)
Dead top	17.3 ($n = 24$)	11.5 ($n = 16$)
Burn scar	15.1 ($n = 21$)	11.5 ($n = 16$)
Cavity in branch	10.8 ($n = 15$)	7.2 ($n = 10$)
Mistletoe	7.9 ($n = 11$)	12.2 ($n = 17$)
Insect infestation	5.0 ($n = 7$)	7.2 ($n = 10$)
Visible fungus/conks	5.0 ($n = 7$)	5.0 ($n = 7$)
Sapsucker holes	2.2 ($n = 3$)	2.2 ($n = 3$)

CHAPTER 3

Characteristics of Den Cavity Microsites and Den Clusters used by Reproductive Female Fishers (*Pekania pennanti*) in the southern Sierra Nevada

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ABSTRACT Tree cavities are important natural resources used by wildlife species worldwide; they provide animals with physical and thermal protection and are often of particularly high value during reproduction. Female fishers (*Pekania pennanti*) are known to use tree cavities as reproductive dens; they give birth in natal dens and most females move their kits to ≥ 1 maternal den over the course of a den season; however, few studies have characterized attributes of tree cavities used by reproductive females including the spatial distribution of the trees with cavities used during a single season (i.e., den cluster). We located reproductive dens of 45 radio-collared

female fishers over 8 reproductive seasons (2008 – 2015), then measured physical attributes of tree cavities at a subset of previously used dens (30 natal, 35 maternal). Measurements were similar for natal and maternal den microsites, with the exception that natal den entrances were smaller than those used as maternal dens (mean vertical x horizontal diameter for natal $11.1 \pm 4.3 \times 7.6 \pm 1.9$ cm versus maternal $19.2 \pm 13.3 \times 9.3 \pm 4.1$ cm). Data from temperature data loggers inside and outside previously used den microsites (20 natal, 21 maternal) during 2013 (late March – June) suggest that den cavities provided good insulation from cold temperatures. Mean daily minimum temperatures were lower outside than inside cavities for all dens; we also found that mean daily minimum temperatures were lower inside cavities used as maternal dens compared to natal dens. Natal den cavity interiors also experienced a smaller proportion of days with temperatures below a cold threshold (5° C) relative to maternal dens. Mean distance between dens used by a female during a den season averaged $364 \text{ m} \pm 314 \text{ SD}$ (range 0 – 1,894 m) and mean distance among all dens used by a female in a single season averaged $930 \text{ m} \pm 650 \text{ SD}$ (range 0 – 2,718 m). Characteristics of den clusters may vary based on local forest conditions and availability of tree cavities, but exploring options to characterize attributes of den clusters can provide land managers with improved information relative to conserving suitable den trees at a spatial scale relevant to fisher reproduction. Buffers around known den clusters based on the mean distance females moved between dens (370 m in our study) may be a reasonable place to start when considering protection or growth of forest patches that could support fisher reproduction in the future.

Key Words: Den, fisher, forest, *Pekania pennanti*, reproduction, tree cavity

1. Introduction

Tree cavities are valuable natural resources used by forest-dwelling wildlife globally (Cockle et al. 2011); these unique habitat elements provide daily refuges for resting and secure locations to care for young during reproduction (Rudolph et al. 1990, Brainerd et al. 1995, Mattson et al. 1996, Kalcounis and Brigham 1998, Hanski et al. 2000, Martin et al. 2004). Some species have the capacity to create their own cavities in live trees, snags, or logs; primary excavators can hollow out cavities in trees of varying hardness while secondary cavity users (or nesters) rely on a combination of primary excavators and natural processes of decay to create suitable cavities (Kalcounis and Brigham 1998, Martin and Eadie 1999, Bonar 2000). While all secondary cavity users are likely to experience challenges regarding cavity availability, cavities suitable for large-bodied animals in this group may be especially rare depending on condition of local trees and occurrence of large primary excavators; if large cavities are locally scarce, they may become a limiting factor for certain species during critical activities like reproduction (Mudappa and Kannan 1997, Bonar 2000, Birks et al. 2005). Because tree cavities develop through processes of decay and the activities of primary excavators in suitable trees (both excavation and transfer of fungi), they can take extensive time and multiple ecological processes to develop (Bednarz et al. 2004, Jackson and Jackson 2004, Remm and Löhms 2011); consequently, they cannot be quickly or easily replaced in forests where old large structures have been removed (Cockle et al. 2011). As both cavities and the trees in which they occur decline over time due to the progression of decay, both also need to be replenished to maintain an adequate supply of cavities (Cockle et al. 2010, Bonar 2000).

Cavities in standing trees (or logs) can provide wildlife with physical shelter from predation as well as thermal protection during inclement weather (Sedgeley 2001, Evans et al.

2002, Law et al. 2013, Grüebler et al. 2014). The height and size of the entrance to such cavities may facilitate survival of young by limiting the number of potential predators that can detect, reach, or access individual cavities (Rendell and Robertson 1989, Wesołowski 2002). Hidden cavity interiors may conceal young and attending parents from view, and the confined cavity chambers may help prevent injuries to young (e.g., falling from tree). Tree cavities can also act as buffers to extreme temperatures (hot or cold) and provide shelter from precipitation (Sedgeley 2001, Paclík and Weidinger 2007). Primary excavators have some choice in the placement of the cavities they use, but secondary cavity users must select from available cavities (Li and Martin 1991, Bonar 2000). Measuring attributes of tree cavities used by wildlife can be difficult, and in some cases, not safely possible; however, when feasible, characterizing attributes of cavities used by wildlife can help identify qualities of importance to individual species, potential benefits of cavity use, and insight into the ecological processes involved in the creation of suitable cavities (Rudolph et al. 1990, Wiebe and Swift 2001, Kahler and Anderson 2006).

The fisher (*Pekania pennanti*) is a forest-dwelling carnivore of conservation concern in western North America that uses tree cavities (and other types of microsites, such as branch clusters) as daily refuges for resting (Zielinski et al. 2004, Purcell et al. 2009); during spring reproduction, however, tree cavities comprise important microsites for denning activities (Paragi et al. 1996, Weir et al. 2012). Fishers have relatively large bodies (females, 2.0 – 2.5 kg, males, 3.5 – 5.5 kg; Powell et al. 2003) compared to many other North American vertebrates that use tree cavities, and they appear to depend entirely on primary excavators and natural processes of decay to form the cavities that they occupy (Green et al. 2017a); consequently, fishers need trees with relatively large diameters and sufficient decay or excavation to yield suitable cavities (Paragi et al. 1996, Powell et al. 2003, Weir et al. 2012). Female fishers give birth in natal dens

in late March or early April, mate within about two weeks of parturition, then generally move their young to ≥ 1 maternal dens while the kits are still nursing and limited in mobility (Matthews et al. 2012, Green et al. 2017b). Female fishers transport kits one at a time to new den structures, and individual females have been documented using 1 to 6 den structures in a single reproductive season (Matthews et al. 2012, Green et al. 2017a). Based on photos from remote cameras at dens, this process appears to become increasingly challenging and risky for females as kits increase in size but remain dependent on the adult female for transport (Green et al. 2017b). Thus, unlike many other forest-dwelling species of conservation concern which use a single site during reproduction (e.g., spotted owl (*Strix occidentalis*), northern goshawk (*Accipiter gracilis*)), fishers require multiple large trees with existing suitable cavities within a reasonable proximity to facilitate safe transport and successful rearing of kits during a single reproductive season (LaHaye et al. 1997, Daw and DeStefano 2001).

Characterizing forest habitat needed by female fishers for reproduction can inform conservation plans; however, some forest features of ecological value to denning females may not be compatible with commonly (or easily) collected measurements or spatial scales generally used in forest management. Specifically, the attributes of cavity microsites and the spatial arrangement of structures with microsites suitable for denning may influence selection of structures by reproductive females including fishers because of their likely connection to survival of newborns (e.g., Neal et al. 1993, Doolan and Macdonald 1997, Rödel et al. 2009). To complement our previous work on the forest structures, sites, and stands used by female fishers for denning in the southern Sierra Nevada (Green et al. 2017a), we thus assessed physical and thermal qualities of tree cavities used as den microsites and the spatial arrangement of all natal

and maternal den structures used by individual female fishers during a single reproductive season (i.e., den cluster).

At the spatial scale of individual den cavities, our objectives were to measure and describe the physical properties of cavities at fisher reproductive den structures (e.g., entrance size, cavity depth) and document the thermal buffering capacity of these microsites relative to ambient temperatures during the denning period; additionally, we wanted to compare physical and thermal properties of cavities used at natal relative to maternal dens. The comparison of natal and maternal den cavity attributes is relevant because fisher kits may be most vulnerable to predation and hypothermia in the first weeks after birth due to their small size during physiologically challenging late winter conditions (e.g., snow, cold temperatures). We hypothesized (H1) that openings of natal den cavities would be smaller than those of maternal dens to prevent entry of larger animals (e.g., predators, adult male fishers). We hypothesized that (H2) all den cavities would help buffer the effects of external cold temperatures, but that (H3) natal den microsites (used earlier in the season) would have greater thermal buffering capacity than maternal den cavities. Although tree cavities used by fishers may have the capacity to provide a buffer to both cold and hot ambient temperatures, our focus was on evaluating thermal buffering capacity during the early part of the fisher den season (late March – April) when cold conditions and late winter storm events might have a disproportionate impact on young kits.

At a broader spatial scale, we investigated the spatial characteristics of fisher den clusters and explored possible applications of these findings to conservation efforts. We quantified basic spatial attributes of den clusters (e.g., distance between dens, distance to nearest neighboring female's active natal den), characterized the area covered by den clusters relative to adult female

home ranges, and developed ideas to integrate this spatial scale into forest planning. As protecting individual known or potential den structures may be insufficient to support successful fisher reproduction, we consider ecologically based buffers relevant to the den cluster spatial scale. Core areas have been identified as areas of high use or importance within animal home ranges (Powell 2000); as den clusters also meet these criteria during the denning season for female fishers, we wanted to determine how buffers (based on distances moved between dens) around den clusters would compare in size with core areas derived from year-round locations. Although core area size may vary by focal species, research question, or techniques used, several studies of wildlife in forested habitats have identified core areas roughly equal to a 30% kernel annual home range (Samuel et al. 1985, Vander Wal and Rodgers 2012, Bowden et al. 2015). Based on previous studies and our understanding of fisher ecology, we hypothesized (H4) that a core area derived from a 30% kernel annual home range for adult female fishers would be comparable in size to an ecologically based buffer of den clusters in our study area.

2. Materials and Methods

2.1 Study Area

Our research was conducted as part of a long-term study of fisher ecology southeast of Shaver Lake, California, USA (37° 3' N, 119° 11' W), in the southern Sierra Nevada. The study area lies on the western slopes of the southern Sierra Nevada and encompasses roughly 43,500 ha of the Sierra National Forest and ranging from 915 to 2,385 m elev. (Fig. 1). In general, precipitation in this region occurs as rain in the fall and snow in the winter at elevations $\geq 1,500$ m. Late winter storms and cold nighttime temperatures can overlap with the timing of parturition and early denning for fishers in our region (late March through April; Green et al. 2017b).

Dominant tree species within the study area included California black oak (*Quercus kelloggii*), canyon live oak (*Q. chrysolepis*), incense cedar (*Calocedrus decurrens*), ponderosa pine (*Pinus ponderosa*), sugar pine (*P. lambertiana*), and white fir (*Abies concolor*). Vegetation within the study area was comprised of lower montane vegetation types such as ponderosa pine-mixed conifer forest, white fir-mixed conifer forest, giant sequoia (*Sequoiadendron giganteum*)-mixed conifer forest (Fites-Kaufman et al. 2007), and montane hardwood forest (Allen-Diaz et al. 2007). Other habitat types present in the area include mixed chaparral at lower elevations (Keeley and Davis 2007) as well as deciduous forest, meadows, rock outcrops, and montane chaparral at middle to high elevations (Fites-Kaufman et al. 2007). Most of the land within the study area is publicly owned and managed by the United States Forest Service, although some areas are privately owned, including large sections managed by the logging company Southern California Edison. Over the last century, management activities on this landscape included timber harvest, prescribed fire, and urban development, although areas of mature forest and patches of large remnant trees were retained. Fire suppression has also led to increases in shade-tolerant tree species (e.g., white fir, incense cedar) and fuels (Fites-Kaufman et al. 2007).

2.2 Capture and monitoring of fishers

We conducted field work from June 2007 through December 2015. We concentrated trapping efforts from October through February and used safe fisher handling methods as described in Green et al. (2017b). To locate individual fishers for home range estimates and find dens of reproductive females in spring, we fitted fishers with radio-collars (model MI-2M, 31 grams, Holohil Systems Ltd., Carp, Ontario, Canada) with hand-stitched breakaway devices (R. Green, unpublished data). For the objectives of this investigation we focused on females which were either adults at the time of the initial capture or would attain reproductive age (≥ 2 years of

age) during the study. We defined a den opportunity as each den season in which a female was old enough to give birth and sufficiently monitored to determine whether she did (or did not) have kits (Green et al. 2017b). We defined a den or rest structure as the live tree, snag, log, or other physical feature used by a fisher to house kits or engage in resting activities; we characterized the den or rest microsite as the fine-scale feature (e.g., cavity, branch) within the structure used by the fisher (Green et al. 2017a).

To estimate annual home ranges of reproductive female fishers, we monitored individuals year-round with ground telemetry and obtained locations using both triangulation and homing techniques (Kenward 2001; see details in Green et al. 2017a). We constrained triangulations of active fishers such that all bearings were obtained within a period of 20 minutes, while triangulations of inactive fishers were not time limited; in both situations, we endeavored to obtain triangulations using ≥ 3 azimuths with $\geq 20^\circ$ differences (Kenward 2001). When possible, we also used homing to identify the specific structure used by resting females that were inactive throughout the course of a triangulation (Green et al. 2017a); if the structure used for resting was confirmed, we used the more accurate location based on homing for home range analyses. If a female left the area as we approached or the signal could not be narrowed to a single structure, we classified the location as a rest area and took coordinates if we had relatively high confidence of being within 50 m of the animal's original resting location (e.g., signal with receiver only, observation of animal running away).

To locate reproductive den structures and associated cavity microsites, we monitored adult females closely from early March through June each year, with an emphasis on morning hours; if a female was inactive, we triangulated a location and used homing techniques to identify potential den structures (Green et al. 2017a). We tried to confirm any potential den

structures with a second visit within a few days of the initial location; we considered a structure used during the spring to be a reproductive den if the female was inactive at the site 2 days in a row, ≥ 2 times in a week, or if kits were documented at the structure. Once a den structure was confirmed, we tried to balance the need to document occupation by the denning female with potential disturbance caused by our presence. In general, we hiked to the den site every 4 to 5 days to confirm that the female was still using the same structure; although we typically confirmed occupancy based on the telemetry signal, we also used evidence from remote cameras (e.g., recent photo of female leaving den without carrying a kit) to verify that the female was still using the structure as a den. On days when we did not hike in to the den site, we endeavored to confirm female presence at dens via remote triangulations or single bearings whenever possible to detect when a female moved to a new structure.

2.3 Physical measurements and temperature monitoring at tree cavities

We located den cavity microsites using a combination of approaches. During visits to active dens, we scanned the structure for possible cavities and used a yagi antenna and receiver to narrow down the specific locations of radio-collared females. In many cases these methods were sufficient to locate den microsites and we noted the location in a sketch or written description on a datasheet for later use. Occasionally we obtained additional confirmation of the cavity location through direct observations of the female fisher poking her head out of a cavity or climbing on the structure near a cavity, or indirect evidence of hairs, fresh claw marks, or signs of recent chewing associated with a cavity; however, most occupied cavities showed little to no sign of being used from ground observations. In some cases, we could not locate the den cavity without climbing the tree. In the early years of the study, we climbed active den structures while the female was away to document litter size (see details in Green et al. 2017b, 2017c); thus, we

confirmed microsites for a subset of den cavities based on presence of kits. For den cavities located during tree climbs outside of the den season (see below), we endeavored to identify the correct den microsite by looking for recent evidence of use (e.g., hairs at entrance) and/or ruling out other possible cavities (i.e., entrance did not lead to a hollow, cavity contained water, etc.).

We obtained physical measurements of cavities at a subset of den structures which were safely accessible, with efforts made to obtain comparable sample sizes of natal and maternal dens. To minimize disturbance, we measured den cavities when structures were no longer being used by the female fisher. Generally, we had to employ tree climbing techniques to measure physical attributes of the cavities, although occasionally microsites were positioned at a sufficiently low height to be accessed directly from the ground or with a short ladder. We followed guidelines to maintain safe conditions for climbers as well as the den cavity and structure, and all climbers completed a tree climbing course taught by United States Forest Service personnel (Berdeen et al. 2015, Green et al. 2017c).

We recorded information on the dimensions of the cavity entrance, interior chamber, and cavity floor, type of entrance (e.g., woodpecker hole, broken limb), and composition of the cavity floor lining (Appendix A). For the dimensions of the cavity opening, we distinguished between actual and functional cavity entrances when obtaining vertical and horizontal measurements; we defined the actual entrance as the physical opening in the tree (e.g., scar, excavation), while the functional entrance was the part of the opening used by the female fisher. In many cases, the actual and functional cavity entrances were equivalent (see Fig. 2a-c); however, especially in microsites which involved a long vertical crack or scar, the functional entrance could be quite a bit smaller than the actual physical opening (see Fig. 2d). We identified the porch as the thickness of the tree wall at the base of the entrance, plus any

additional portion of wood or broken limb sticking out from the tree when present; the porch measurement was taken from the outer lip of the lowest point where the fisher entered the cavity to the point where the hollow began inside the entrance (See Appendix A). We measured interior diameter from the bottom of the entrance to the back wall of the hollow; when possible, we took a second interior diameter measure perpendicular to the first measurement. We measured depth beginning at the bottom of the functional entrance to the bottom of the hollow chamber; in shallow chambers this could be measured with a collapsible ruler, while at deeper cavities we tied a carabiner to a string, lowered the carabiner to the cavity floor, and then measured the length of the string. For cavity floor diameter, we measured the widest section of the floor, then took a second perpendicular measurement. Additionally, we calculated the area of an ellipse for the functional cavity entrance and the chamber floor (equation = $\pi * (D1/2) * (D2/2)$; where D1 and D2 are the perpendicular diameters).

Outside the cavity, we measured tree diameter at the cavity entrance and at the cavity floor. Because cavities varied in shape, size, and accessibility, different tools were required for interior measurements in different cavities, including flexible, stiff, and collapsible rulers, a diameter tape, and a small digital camera; for deep cavities, we often used a homemade cavity camera that we developed to count kits (see Green et al. 2017b); this consisted of a security camera, a long flexible handle, a battery pack, and a handheld video camera which allowed us to look inside the cavity and record video. Floors of cavities deeper than approximately 0.5 m generally could not be accessed directly for measurement; for such cavities, we estimated diameter from photos or video of the cavity floor with a ruler in the view for scale.

Between late March and early April 2013, we deployed HOBO temperature/light data loggers (model UA-002-64; Onset, Bourne, MA) at 18 natal and 20 maternal den structures

located during previous den seasons (2008 – 2012). We deployed two loggers at each structure, one to measure ambient temperature and one to measure temperature inside the cavity. We fastened the exterior logger to a metal bracket and nailed the bracket to the east side of the tree bole outside the den cavity within 1 m of the entrance; this positioning standardized exposure of the loggers to sunlight across dens. We hung the interior logger inside the cavity by a polyethylene cord secured to the metal bracket of the external logger or with thin copper wire (Appendix A). To avoid obstructing animals that might enter or use the tree cavity, we attempted to secure the cord or wire in a manner that avoided blocking the cavity entrance. We positioned the internal logger such that it was just at or above the cavity floor in a location that represented the cavity conditions, but reduced the chance of an animal in the cavity altering the thermal data by sitting on or leaning against the logger.

We programmed loggers to collect temperature and light data every 10 minutes to document daily variability and extreme conditions. Loggers were then deployed for the duration of a normal den season, although placement dates were staggered between 23 March and 17 April due to logistical constraints; however, most of the loggers were set up over dates which closely overlapped the time period when female fishers in our study area initiated dens. We retrieved loggers in the fall of 2013 and downloaded data using HOBOWare software (Onset, Bourne, MA). In two cases the internal logger had been pulled out of the cavity by an animal when we revisited the site; however, we could identify the date this occurred based on the light exposure data, allowing us to exclude data from dates during which the logger was exposed to ambient temperatures. At three dens, at least one logger was sufficiently damaged by an animal that data could not be recovered and in one case a logger was missing; data from these paired loggers were excluded.

We truncated data for this study to include only the time period between 1700 on the day of field deployment and 2350 on 30 June 2013. We used HOBOware Pro (Onset, Bourne, MA) to summarize hourly minimum, mean, and maximum temperatures. We separated temperature data into early (late March and April) and late (May and June) den season for some summaries and analyses. Early den season dates corresponded with the period of time that most female fishers used natal dens (mean date of first move from maternal den 27 April; Green et al. 2017b). During the early den season, fisher kits were still young, small, and likely more vulnerable to cold temperatures than during the late den season. Additionally, the early den season overlaps with periods of late winter conditions (i.e., snow storms, cold temperatures). Within each time period we compared thermal buffering capacity of natal and maternal dens by calculating T_a (ambient temperature) – T_d (den cavity temperature) for daily minimum, mean, and maximum temperatures. We compared natal and maternal dens in terms of their relative buffering capacity.

To provide context for the temperature data that we collected at dens in 2013 relative to all years that we monitored fisher reproduction, we summarized data from a weather station located in the northwestern portion of our study area. Data were obtained for the Shaver Lake site from the National Centers for Environmental Information (<https://www.ncdc.noaa.gov/cdo-web/>); using the global summary of the month option, we focused on months that overlapped the fisher denning season (March – June) and averaged temperature data across years included in our den monitoring efforts (2008 – 2015; Appendix B). The mean elevation of reproductive dens located during our study was about 250-m lower than the Shaver Lake weather station, however, these temperature data reflect the relative pattern over all the years of the study; moreover, the range of elevations at dens (1,013 – 2,059 m) included the elevation of the station (1,751 m).

We calculated the number of hours that fell below 5° C relative to the total number of hours monitored at natal and maternal dens to assess potential differences in the amount of time kits might be exposed to exceptionally cold temperatures during early denning. We used 5° C as a threshold because temperatures below this threshold have been used in experiments associated with cold stress in small mammals comparable in size to young fisher kits (e.g., Lončar et al. 1988, Moore et al. 2001). As the den attendance patterns of female fishers may be influenced by thermal conditions at dens, particularly cold temperatures when kits are young (Cummings 2016), we also identified the hour with the coldest mean temperature for each day that we had temperature data at individual natal dens in late March and early April; we then calculated mean coldest times by date across natal dens to show patterns of daily extremes for temperatures inside and outside den cavities. Occasionally, multiple (and usually sequential) hours had the same cold temperature value; as we were primarily interested in how cold temperatures might influence when females leave the kits to go foraging, we selected only the latest hour in those instances. We graphically summarized minimum and mean internal and external temperatures across the full den season to highlight normal thermal patterns relative to extreme cold events; additionally, we noted the dates and times when the most extreme events occurred and provided a graphical example of conditions from one natal den and one maternal den to better describe thermal patterns during these events.

2.4 Characterization of home ranges and den clusters

We calculated annual home ranges (e.g., January through December) for a subset of adult female fishers each year. We used a normal calendar year because we felt it adequately represented a female fisher's movements relative to their reproductive cycle; e.g., pre-denning period (January – late March), the full denning period (late March – June), the mobile kit rearing

period (July – October), and the presumed period of separation from kits (October – December; Green et al. 2017b). For each year, we calculated home range for females who were ≥ 2 years of age by the beginning of the associated spring denning season, had attempted to den, and were monitored for the full den season. We included locations from triangulations, rest structures, rest areas, and den structures. Triangulated locations were included only if their error polygons were below a threshold size of 107,000 m² (10.7 ha). We determined this criterion by calculating the distance between actual and triangulated locations of rest and den structures ($n = 650$) for which we had these paired data, then used the mean distance between known and estimated locations as the radius for our error polygon threshold. Note that this area represents approximately 0.6 – 0.7% of the mean home range size for adult female fishers in our study. Last, because our objective was to compare characteristics of the den cluster to the area used by females year-round (e.g., not to assess differential use of the home range), we used only the initial detection of a female at a reproductive den location in generating an annual home range (e.g., we did not incorporate multiple uses of a given structure); a rare exception was when a female either moved kits away from the den then moved back, or when a female used the location for resting outside of the den season (also used as a second location). Finally, we only generated home ranges for reproductive females for which we had a minimum 20 locations and 6 months of monitoring effort for a given year, comparable to methods used by Lewis et al. (2016).

After narrowing our location data to meet the above criteria, we used ArcGIS (ESRI, Redlands, CA) to create shapefiles of locations for each individual female in each year that fit our criteria. We used the *adehabitatHR* package in R version 3.2.2 (R Core Development Team 2015) combined with location and date in shapefiles to generate home ranges using the fixed-kernel method at 30% and 95% utilization distributions to represent the annual core and home

ranges of female fishers respectively. We selected the “reference” smoothing factor (Href) and used default settings for grid and extent.

We used ArcGIS to calculate total distances moved between dens in a cluster using the *points to line* tool and used the *split lines at vertices* tool to calculate distances moved between individual dens. We used the *minimum bounding geometry* tool to calculate the area of a polygon encompassed by den clusters with ≥ 3 den structures. We also generated buffers around den clusters based on the mean distance traveled between dens and calculated the area of these associated polygons to compare with the area of home range kernels.

2.5 Statistical analysis

We compared physical measurements of tree cavity microsites at natal dens to those at maternal dens using *t*-tests or non-parametric tests as appropriate. For some comparisons, data were transformed using a log, squared, or cubic function to yield data with a normal distribution for use in statistical tests. To evaluate the thermal buffering capacity of den cavities, temperature data were categorized to facilitate three different comparisons: cavity interior relative to paired cavity exterior, natal den relative to maternal den, and early den season relative to late den season. We compared daily minimum, mean, and maximum temperatures between natal and maternal dens within the early and late den periods using *t*-tests to assess differences in thermal buffering capacity. To assess differences in temperature between ambient and cavity temperatures, we also used paired *t*-tests to compare daily temperature data (minimum, mean, maximum) from inside and outside of den cavities within the same den group (natal, maternal) and time period (early, late). Last, to evaluate differences in the amount of time that kits might be exposed to cold temperatures at natal compared to maternal dens during early denning, we calculated the number of hours that fell below 5°C at each den relative to the number of hours

monitored, averaged across sites, and compared the resulting proportions between groups using *t*-tests. We performed statistical tests using NCSS 11 Statistical Software (NCSS, LLC, Kaysville, Utah) and home range analyses in R version 3.2.2 (R Core Development Team 2015).

3. Results

3.1 Fisher captures and monitoring efforts

Between June of 2007 and December of 2015, we captured 72 female fishers, 52 of which were monitored as adults during ≥ 1 denning season. Over 8 reproductive seasons (2008 – 2015), we confirmed 45 of these females at ≥ 1 reproductive den; we also documented 111 denning opportunities during which individual female fishers were ≥ 2 years of age and sufficiently monitored to determine reproductive activity.

3.2 Fisher den cavity measurements

We collected physical measurements at a subset ($n = 65$; 30 natal dens and 35 maternal dens) of the den structures located during the project ($n = 275$; see Green et al. 2017a). Tree species of dens where we collected cavity measures included California black oak (22 natal, 28 maternal), incense cedar (4 natal, 5 maternal), ponderosa pine (2 natal), and white fir (2 natal, 2 maternal). Due to accessibility and safety concerns, we climbed a higher percentage of California black oaks and lower percentage of white firs than were used as den trees, and we did not climb any snags (see Green et al. 2017a); consequently, most of the den trees measured were alive (92.3%; 28 natal, 32 maternal), with the exception of a few snags with cavities accessible from the ground or neighboring live trees (7.7%; 2 natal, 3 maternal). Cavity entrances at dens where we collected measurements were formed by limbs breaking off the trunk (80.0% natal, 65.7% maternal), woodpecker excavation (16.7% natal, 17.1% maternal), and other factors

including burn scar, broken trunk, and vertical crack on the side of the bole (3.3% natal, 17.1% maternal; see Fig. 2).

Measurements of functional entrances at natal den cavities were more restrictive than those of maternal dens; specifically, vertical measures and calculated area of ellipses at entrances were smaller at natal than maternal den cavities ($P < 0.01$), while horizontal measures of den entrances tended to be narrower for natal than maternal dens ($P = 0.06$; Table 1). Across all dens, horizontal measurements at both functional and actual entrances were narrower than vertical measures (respectively, $t_{63} = 6.4$, $P < 0.01$; $t_{63} = 0.27$, $P < 0.01$). Additionally, mean vertical measures at actual entrances were over twice as long as functional entrances (42.2 cm versus 19.2 cm; Table 1), generally because females could only fit through a restricted opening along the scar (see Fig. 2d). Other attributes associated with cavity measurements did not differ between natal and maternal dens, including interior diameter, porch thickness, or diameter of the chamber floor (Table 1). Although depth of cavity interior did not differ between natal dens and maternal dens, measurements of this attribute did show considerable variation, with depths ranging from 142.4 – 5256.4 cm at natal dens and 393.8 – 9545.6 cm at maternal dens.

Den cavity floors generally were lined with at least a thin layer of material (Fig. 3e), although we observed no evidence that female fishers brought lining into the den chamber; materials found on the cavity floors of natal ($n = 20$) and maternal dens ($n = 22$) respectively included combinations of shredded wood (70%, 59%), small wood chips (55%, 64%), chunky wood blocks (20%, 32%), conifer needles (0%, 5%), deciduous leaves (5%, 27%), remains of chewed pine cones (5%, 9%), and bark (5%, 0%). Depth of lining was difficult to quantify in many cavities; where it could be measured, mean depth of lining in natal dens was 7.1 cm (± 11.3 SD, range 0.5 – 30.0) and in maternal dens was 8.4 cm (± 9.0 SD, range 0.5 – 24.8).

Diameter of trees at the cavity entrance and at the chamber bottom also did not differ between natal and maternal dens (Table 1); however, measurements at both natal and maternal dens reflected the large size of these trees, with mean diameter near cavities > 67 cm and mean diameter at breast height > 80 cm.

3.3 Temperature monitoring at fisher den cavities

Of 38 pairs of temperature loggers deployed at dens (18 natal, 20 maternal), we recovered data from logger pairs at 15 natal and 19 maternal dens. Across all dens (natal and maternal combined), temperatures inside cavities fluctuated less than did external temperatures (Fig. 4a). In general, daily minimum temperatures inside den cavities did not drop as low as paired external minimum temperatures (Fig. 4a, Table 2); in contrast, mean temperatures outside of dens typically remained higher than those within dens (Fig. 4a, Table 2). Temperatures were generally lower in the early den season (late March – April) compared to the late den season (May – June), reflecting the occurrence of several late winter storms and lower daytime temperatures during this period (Fig. 4a, Table 2).

Daily internal minimum temperatures during both the early and late den seasons were higher at natal compared to maternal dens (early $t_{32} = -2.34$, $P = 0.03$; late $t_{32} = -2.60$, $P = 0.02$; Table 2); daily mean and maximum temperatures did not differ between natal and maternal dens in either season. The absolute lowest temperatures recorded inside cavities during the early and late denning periods were also higher at natal dens compared to maternal dens (early $t_{32} = -2.44$, $P = 0.02$; late $t_{32} = -2.08$, $P = 0.05$; Table 2, see example Fig. 4b), whereas external temperatures did not differ between den types in either season. In assessing the relative amount of time kits might be exposed to cold temperatures during the early denning period, temperature loggers in natal dens recorded a smaller proportion of hours with critically low temperatures (<5° C)

compared to maternal dens ($t_{31} = 2.56$, $P = 0.02$, Fig. 5). As might be expected, interior temperature loggers had a smaller proportion of monitored hours below 5° C than paired external loggers at both natal and maternal dens (natal $t_{13} = -4.56$, $P < 0.01$; maternal $t_{18} = -3.71$, $P < 0.01$), whereas external temperatures did not differ between natal and maternal dens.

Across 15 natal dens for which we identified the coldest hour of each day in the early den season, the absolute coldest hours generally occurred earlier outside the cavity (mean 0714, ± 4 hours 40 min SD compared to inside the den cavity (0948, ± 3 hours 33 minutes SD); these general times and pattern of delayed cold internal temperatures stayed relatively consistent across the early season, with a few nighttime exceptions that may have been associated with individual storms (Appendix C). While 2013 exhibited a slightly warmer temperature pattern compared to mean values across all years of our study (Appendix B), we did document thermal patterns at den cavities during a few late winter storms.

The buffering capacity of dens was particularly notable during a storm that occurred between 16 and 17 April (Fig. 4a). Measurements taken from 14 – 18 April highlighted the thermal stability provided by dens, but especially by natal dens (2-3°C warmer than maternal dens); in addition to thermal buffering these dens delayed the intrusion of cold temperatures by 2.5 to 3 hours (times rounded to the nearest 10 min interval, natal external mean 750, internal mean 840, mean lag time 2 hours 50 min; maternal external mean 710, internal mean 830; mean lag time 2 hours 40 min; see example Fig. 4b).

3.4 Characteristics of fisher den clusters and associated home ranges

Between 2008 and 2015, we monitored 81 successful opportunities to reproduce by 39 female fishers. On average, females used 3.4 den structures in a denning season and moved 2.6 times between dens (Table 3, Fig. 6). Rarely ($n = 4$), a female would stay in the same structure

for the entire den season; on 2 of these occasions the females were known to be reproducing for the first time. Females moved an average of 364 m between individual den structures, with a mean distance of 930 m across all dens over the full season (Table 3). For den clusters with ≥ 3 den structures, the minimum convex polygon created by the locations of these structures was 10.5 ha (Table 3). We calculated a buffer of 370 m (based on the mean distance between dens, rounded up to the nearest ten) and applied this around all den clusters with ≥ 2 dens; the mean area encompassed by the resulting polygons was 107.8 ha; for comparison, mean area of fisher core areas (30% fixed-kernel home range estimates) was 150.9 ha and that of 95% fixed-kernel estimate was 1469.3 ha (Table 3). The mean distance from each natal den to the nearest neighboring female's natal den known to be active within the same season was 2,597 m, with a median value of 2,385 (Table 3).

Although we found similarities in den cluster spatial patterns across females and years, we also found variability. We present examples of den clusters for 2 females (F27, F28) that reproduced in 4 consecutive seasons to demonstrate both consistency and variability among individual female fishers in our study area (Fig. 7). For visual reference, we show both the convex hull (i.e., minimum convex polygon formed by connecting lines between all the dens used in a season by a female) as well as the 370 m buffered polygons associated with each den cluster; in these examples, the den clusters of both females fell within a relatively compact area during their first two years of denning, involved a larger area in their third year of denning, then shrank again in size in their fourth den season. Both females also denned in one stream drainage for two seasons, then switched to neighboring drainages for subsequent seasons; the behavior of showing fidelity to a moderately small forest patch for a year or two, then moving to a neighboring patch of forest was not uncommon for females monitored for multiple years. Of

note, in the example for F27, a second female (F26, thought to be F27's daughter) began denning in the first drainage used by F27 after she moved to the second drainage in 2011.

4. Discussion

All field studies of fisher reproductive habitat have highlighted the use of tree cavities as den microsites for reproducing females, and they have emphasized the important role of large decayed structures with cavities in the conservation of this species (Paragi et al. 1996, Weir et al. 2012, Green et al. 2017a). Our study sheds additional light on the physical and thermal attributes of tree cavities that may help explain their function as key habitat elements during fisher reproduction. Although we documented many similarities in natal and maternal den cavities, our work highlights some key differences, such as entrance size and thermal properties, that may be tied to kit survival. Our findings also indicate that some attributes of den cavities may be influenced by or related to fisher behavior during the reproductive period, including male visitation to natal dens during the mating period and den attendance patterns by individual females in the early den season. Finally, our descriptions of the physical characteristics of tree cavities used as den microsites and the spatial distribution of den clusters in forested landscapes can be incorporated into field identification of potential den structures and conservation of suitable habitat at spatial scales of relevance for fisher reproduction and landscape management.

4.1 Physical Characteristics of Fisher Den Cavities

One of our most interesting findings, related to the physical properties of tree cavities used as dens by female fishers, was tied to our first hypothesis (H1), that the openings of natal den cavities would be smaller than those of maternal dens to restrict entry of larger animals (e.g., predators, adult male fishers). To the best of our knowledge, the idea that females might select tree cavities with smaller entrances during the early denning (and mating) period to protect kits

from large-bodied adult males was first presented by Leonard (1980) and emphasized again by Paragi et al. (1996), but neither of them were able to test this idea. In our study area both the vertical measures and ellipse calculations at cavity entrances were smaller at natal than maternal dens, with horizontal measures following a similar pattern; these findings support our hypothesis and the points made by previous researchers. As the mating period should be over by the time that most females moved to maternal dens in our study area, there may no longer be a need to exclude males at this point. Photos and observations of females entering natal dens indicate that they barely fit through some of these entrances (see Fig. 3 a, b), suggesting that subadult and adult male fishers, which have broader heads and chests, likely would be excluded. For reference, body measurements relevant to cavity entrance size obtained at captures on our project for adult females ($n = 48$ individuals) were consistently smaller than those of adult male fishers ($n = 26$ individuals); specifically, a comparison of mean values for zygomatic arch (female $5.7 \text{ cm} \pm 0.4$, male $7.6 \text{ cm} \pm 0.6$), head circumference (female $18.5 \text{ cm} \pm 0.8$, male $24.8 \text{ cm} \pm 1.4$), and girth (female $21.6 \text{ cm} \pm 1.4$, male $28.0 \text{ cm} \pm 2.0$) all support the idea that males could be excluded from small cavities that may be still be accessible to females. We emphasize that anecdotal observations of male fishers at natal dens over the course of our research (Green et al. 2017b), records from captive settings (Hodgson 1937), and general understanding of fisher reproductive ecology (Powell et al. 2003) do not indicate that males would purposefully kill young fishers, but kits could be at risk of accidental injury or suffocation if mating were to occur within the confined space of a tree cavity.

Although exclusion of males seems to be the most compelling reason for females to select natal den cavities with small entrances, other factors may also influence den microsite selection. Small entrances at natal dens may allow females some degree of selection in mating

opportunities, as they may choose whether or not to exit the cavity to mate if a male visits the den tree. Small openings certainly limit access of other potential predators (e.g., black bear (*Ursus americanus*), bobcat (*Lynx rufus*), gray fox (*Urocyon cinereoargenteus*)). And, larger entrances at later maternal dens may facilitate moving larger but still-dependent kits.

Additionally, our data suggest that cavities with smaller entrances may be associated with increased insulation, reduced heat loss, and greater thermal buffering, all of which may be more important earlier in the den season. As these explanations are not exclusive of each other, they may all have some influence on the cavities female fishers select for denning.

Other than entrance size, physical measurements of den cavities were not noticeably different between natal and maternal dens. Depth of cavities was quite variable (Table 2), but averaged just under 1 meter (natal dens) to nearly 1.5 m (maternal dens), such that kits and nursing females were usually out of view and protected from precipitation. Our ability to measure depth of lining was limited, but observations of lining types and limited data on depth suggest that this material may provide some degree of visual and thermal cover for kits (Fig. 3e). Last, measures of tree diameter reflected the relatively large size of trees associated with suitable fisher den cavity microsites.

Few studies have described the physical properties of cavities used as reproductive den microsites by female fishers (Paragi et al. 1996, Weir et al. 2012); no previous studies have characterized fisher den microsites in the southern Sierra Nevada where dominant tree species differ. Whereas fishers in other parts of the range frequently use quaking aspen (*Populus tremuloides*), balsam poplar (*P. balsamifera*), and red maple (*Acer rubrum*) female fishers in our study area used California black oak more than any other tree species for reproductive den structures, followed by white fir and incense cedar (Green et al. 2017a). Most den cavity

entrances in California black oaks in our study appeared to be created by a single large limb breaking off and providing access to a hollow in the main trunk (McDonald 1990). Hardwood tree species such as California black oak tend to develop heart rot more readily than conifer species, which may help explain the dominance of hardwoods as fisher den structures (McDonald 1990). Some cavity entrances in conifers also appeared to be formed by broken limbs or scars combined with heart rot, but others were clearly formed by woodpeckers. Cavity measurements in conifer snags were somewhat underrepresented in our measurements because we did not climb dead trees; thus, entrances created by woodpeckers may be also be underrepresented, although we did measure a few cavities in safely accessible snags, including some with woodpecker activity (see Fig. 2b, Fig. 3a, b).

Woodpeckers are the most common and influential primary excavators in forests, but woodpecker species vary in their capacity to excavate and in the size of the cavities they produce. In North America, the pileated woodpecker (*Dryocopus pileatus*) excavates cavities in trees for nesting and roosting that are later used by a wide variety of birds and mammals (Bonar 2000); because of their large size and widespread distribution, pileated woodpeckers play an especially important role in contributing to cavity availability in forested habitats. The two largest woodpeckers that occur in our study area are the pileated woodpecker and northern flicker (*Colaptes auratus*); both of these species will excavate nest cavities in trees where fungi associated with heart rot are present (Conner et al. 1976). Entrances to nest cavities excavated by pileated woodpeckers are comparable in size to those used by fishers as natal dens (mean vertical x horizontal diameter: Oregon, 12 x 9 cm; Virginia, 9.6 x 9.2 cm; New York, 10.5 x 8 cm; Bull and Jackson 2011). However, nest entrances excavated by flickers generally appear to be too small for use by fishers (Ohio, 8.2 x 7.3 cm (Ingold 1994); Wyoming, 6.58 cm (only one

diameter reported; Gutzwiller and Anderson 1987); British Columbia, 7.5 x 6.9 cm (Peterson and Gauthier 1985); central British Columbia, 6.45 cm (only horizontal diameter reported; Wiebe and Moore 2008). Thus, the creation and conservation of tree cavities suitable for fisher reproduction may be facilitated by encouraging ecological processes that lead to the growth of large limbs and heart rot (particularly in California black oaks) along with the maintenance of pileated woodpecker populations within elevations used by fisher. Finally, while not all woodpecker species create cavities large enough for fishers, daily activities of multiple woodpecker species can spread fungi that may lead to tree decomposition and eventually to cavities and snags of use to fishers (Farris et al. 2004).

4.2 Thermal Characteristics of Fisher Den Cavities

Based on weather patterns observed during the first few years of our fisher den monitoring efforts, and anecdotal information on field conditions during reproduction from other parts of the range, we expected (H2) all den cavities to provide some level of protection against extreme ambient temperatures (see Thompson and Purcell 2016); however, we additionally hypothesized that (H3) natal den microsites would have a greater thermal buffering capacity than maternal den cavities, particularly during the coldest portions of the denning season. Fisher kits are very small and they are born hairless (Powell et al. 2003), so they are presumably quite vulnerable to exceptionally cold temperatures or prolonged exposure to moderately cold temperatures. Other researchers have documented associations between unseasonably cold temperatures and mortality in young mammals and birds (Neal et al. 1993, Doolan and Macdonald 1997, Rödel et al. 2009); these studies suggest that late winter storms may also present increased risk of death for young fisher kits. During the early denning period, reproductive females may select microsites and structures with characteristics that minimize

risks associated with cold temperatures (e.g., well-insulated cavities, cavities with greater exposure to warmth from the sun). It is no surprise that temperature loggers deployed at den cavities confirmed that these microsites buffer cold external temperatures; more interesting is that natal dens exhibited greater thermal buffering capacity than maternal dens, particularly during the coldest days of the den season. These findings further emphasize the value of tree cavities to female fishers during the reproductive process, and suggest that selection of cavities with specific characteristics may be associated with higher kit survival.

While thermal properties of cavities may benefit kits and resting females directly by reducing exposure to extreme or lengthy cold temperatures, these properties may also allow lactating females more flexibility as to when and for how long they can be away from the kits to forage during the early den season. Our field observations suggest that female fishers tend to be at natal dens most regularly in the early morning hours, which correspond to some of the coldest external and internal temperatures observed at dens during this study (Appendix C).

Additionally, female fishers spend more late night and early morning hours at dens when temperatures are likely to be cold (Cummings 2016). Female fishers likely use their own body warmth to help kits survive the most extreme daily and seasonally cold temperatures, so any additional thermal buffering that can be gained through selection of optimal cavity microsites may help reduce their energetic costs. One implication of these observations is that human activities that might keep females from their dens overnight should be particularly discouraged early in the den season (e.g., March – April). Three observations made here have additional conservation implications relative to research and management activities. First, females appear to select cavities that buffer from cold temperatures; second, we documented some relatively cold temperatures inside and outside of den cavities in our study area; third, females often are at

dens during times when temperatures may be coldest (Cummings 2016). Together these observations suggest that human activities (including live-trapping for research) that could keep females from their kits overnight during the early den season in particular might put kits at risk.

4.3 Spatial Characteristics of Fisher Den Clusters

Female fishers differ somewhat in their behaviors and habitat requirements relative to other forest-dependent species of conservation and management concern (e.g., spotted owl, northern goshawk). First, they require tree cavities with specific physical and thermal properties. Second, they require multiple structures with suitable cavities each season (e.g., den clusters), and may (or more frequently, may not) use the same structures for reproduction in subsequent years. Third, den structures need to be within a reasonable distance of each other to facilitate transport one or more kits to new dens as needed. Biologists and forest managers aiming to conserve habitat suitable for fisher reproduction need to integrate these factors and the unique spatial scale of known den clusters into their planning process. We documented information on distances that females moved kits between individual dens, total distances moved between dens in a season, and proximity of active natal dens in a given year. While these findings may not represent the full spectrum of distances that females could move young and patterns could vary in landscapes with different forest conditions, we hope they provide some reference points for conservation planning and will help facilitate further discussion on this topic.

To our knowledge, we present one of the first assessments of the spatial distribution of den structures used by female fishers in a given season; while characteristics of den clusters are likely to vary with the availability of suitable trees with cavities, understanding the area encompassed by a den cluster is essential for managers hoping to conserve potential den trees at a spatial scale relevant to fisher reproduction. The use of a buffer around known den clusters

that is compatible with the mean distance females moved between dens (370 m in our study) may be a reasonable place to start when considering protection or growth of forest patches that could be used for fisher reproduction in the future. We hypothesized (H4) that the mean area encompassed by a den cluster would approximate the 30% core area. Using a 370-m buffer around dens yielded an area that was approximately 71% of the 30% fixed-kernel annual home range (respectively, 107.8 ha versus 150.9 ha; Table 3), corresponding approximately to a 21% “core” area. Therefore, where reproductive den structures have not been identified but home range data are available, determining the area of 25% to 30% fixed-kernel home ranges might be a reasonable estimate of a suitable spatial scale to conserve and create clusters of potentially suitable den structures and associated habitat. We also documented female fishers establishing natal dens at a considerable distance (mean of 2.6 km) from natal dens of the closest neighboring reproductive females (Table 3) as well as individual females moving to different drainages between years. Although this topic warrants further investigation, these findings are also important for conservation planning as they suggest that forest patches containing potentially suitable den clusters may need to be broadly distributed across the landscape for them to be of greatest use to the local fisher population.

5. Conclusions

Our results reinforce the critical value of tree cavities for fisher reproductive ecology and the need to maintain the biological processes and physical structures that lead to appropriately sized cavities for female fishers. Our results support existing hypotheses about the physical and thermal benefits of tree cavities to female fishers and provide specific values associated with physical measurements that may facilitate conservation of suitable tree cavities in forested habitats where fishers occur. We also emphasize the role fisher behavior appears to play in the

selection of den cavities, from the use of cavities with small entrances at natal dens to patterns of den attendance that may be closely tied to the thermal buffering capacity of den cavities. Last, we encourage further exploration of the characteristics and distribution of den clusters as this approach may provide a new perspective on finding ways to manage forests while still conserving forest patches with potential den structures (i.e., large trees with cavities) at a spatial scale that can best facilitate successful fisher reproduction.

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Table 1. Summary of measurements collected at a subset of tree cavities used by female fishers as reproductive den microsites in the southern Sierra Nevada between 2008 and 2015. Descriptions of measures are in Appendix A. We used a Bonferroni-adjusted P value of 0.003 for significance, reflecting an alpha value of 0.05 and 15 tests; bold letters denote statistical differences.

Den Cavity Measures (in cm unless noted)	Natal Dens			Maternal Dens			Tests
	Mean (\pm SD)	Range	n	Mean (\pm SD)	Range	N	
Entrance							
Functional - vertical	11.1 \pm 4.3	5.0 – 24.0	30	19.2 \pm 13.3	7.0 – 69.0	34	$t_{62} = 3.92, P < 0.003$
Functional - horizontal	7.6 \pm 1.9	5.0 – 12.0	30	9.3 \pm 4.1	5.0 – 23.0	34	$t_{62} = 1.93, P = 0.06$
Functional ellipse (cm ²)	65.2 \pm 26.2	29.8 – 146.0	30	139.9 \pm 138.9	41.2 – 812.5	34	$t_{62} = 4.76, P < 0.003$
Actual - vertical	18.2 \pm 16.0	5.0 – 70.5	30	42.2 \pm 69.4	7.8 – 306.0	34	$t_{62} = 2.52, P < 0.014$
Actual - horizontal	9.5 \pm 4.8	3.0 – 26.5	30	9.7 \pm 4.9	4.0 – 31.0	34	$t_{62} = 0.34, P = 0.74$
Porch thickness	8.8 \pm 4.4	1.5 – 19.0	30	11.0 \pm 6.9	1.0 – 27.0	34	$t_{62} = 1.53, P = 0.13$
Interior							
Diameter - front to back	25.0 \pm 13.0	8.4 – 54.0	27	28.4 \pm 14.2	9.0 – 76.0	32	$t_{57} = 1.10, P = 0.28$
Diameter - perpendicular	23.9 \pm 13.6	5.4 – 50.0	26	25.7 \pm 12.7	10.0 – 53.0	28	$t_{52} = 0.85, P = 0.40$
Depth	87.0 \pm 70.0	8.0 – 382.0	29	135.9 \pm 147.7	4.0 – 800.0	32	$t_{59} = 0.55, P = 0.59$
Cavity floor							
Width - widest	36.2 \pm 8.5	21.0 – 56.0	23	34.6 \pm 14.2	10.0 – 75.0	20	$t_{41} = -0.45, P = 0.65$
Width - perpendicular	27.5 \pm 8.7	12.0 – 46.0	23	29.8 \pm 10.0	10.0 – 46.0	20	$t_{41} = 0.81, P = 0.42$
Ellipse (cm ²)	814.1 \pm 444.7	346.2 – 2022.2	23	918.3 \pm 597.0	78.5 – 2472.7	19	$t_{40} = 0.65, P = 0.52$
Tree diameter							
At base of entrance	66.3 \pm 15.1	43.0 – 92.4	28	70.5 \pm 27.3	28.9 – 182.0	34	$t_{60} = 0.34, P = 0.73$
At base of chamber	67.6 \pm 14.1	40.7 – 94.7	27	69.9 \pm 32	28.9 – 125.5	32	$t_{57} = 0.52, P = 0.61$
At breast height	80.8 \pm 26.7	40.1 – 153.2	30	81.9 \pm 22.0	49.5 – 143.2	35	$t_{63} = 0.39, P = 0.70$

Table 2. Summary of temperature data recorded by loggers at tree cavities previously used as reproductive dens in the Kings River study area (located 2008 – 2012). Loggers were deployed for the 2013 den season at unoccupied den trees. Data were grouped into early den season (late March through April) and late den season (May and June). We calculated mean hourly temperatures from data collected every 10 minutes, then determined mean daily temperatures (minimum, mean, maximum); the resulting mean values and standard deviations were averaged across dens based on type (natal, maternal) and season (early, late). Minimum temperatures were identified for each day that a logger was deployed, then averaged by category. We used a Bonferroni adjusted P value of 0.003 for significance; bold letters denote statistical differences between internal (Ti) and ambient temperatures (Ta).

Measures Grouped by Season and Den Type	Interior Temperature C° (Ti)		Ambient Temperature C° (Ta)		Ti - Ta (C°)		Tests
	Mean ± SD	Range	Mean ± SD	Range	Mean ± SD	Range	
Early den season							
Natal den cavity							
Daily minimum	9.4 ± 4.0	7.1 – 15.5	6.1 ± 4.3	3.2 – 14.2	3.3 ± 1.4	0.8 – 6.1	<i>t</i>₁₄ = 8.02, <i>P</i> < 0.003
Daily mean	11.3 ± 4.0	7.9 – 17.7	11.9 ± 4.6	9.0 – 17.7	-0.6 ± 1.8	-2.9 – 0.6	<i>t</i> ₁₄ = -2.94, <i>P</i> = 0.01
Daily maximum	13.6 ± 4.2	8.5 – 21.2	25.8 ± 7.6	13.3 – 31.7	-12.1 ± 5.4	-21.7 – -2.1	<i>t</i>₁₄ = -9.45, <i>P</i> < 0.003
Minimum record	1.2 ± 2.4	-2.0 – 6.7	-2.7 ± 2.9	-4.8 – 7.2	---	---	<i>t</i>₁₄ = 6.32, <i>P</i> < 0.003
Maternal den cavity							
Daily minimum	7.8 ± 4.1	5.3 – 11.2	5.2 ± 4.1	3.9 – 7.3	2.7 ± 0.9	0.6 – 5.6	<i>t</i>₁₈ = 7.38, <i>P</i> < 0.003
Daily mean	10.2 ± 4.1	8.0 – 12.2	11.1 ± 4.6	8.6 – 13.1	-1.0 ± 1.4	-2.4 – 0.0	<i>t</i>₁₈ = -6.21, <i>P</i> < 0.003
Daily maximum	12.9 ± 4.3	9.7 – 17.3	24.5 ± 7.3	13.4 – 32.1	-11.5 ± 4.4	-18.3 – -2.1	<i>t</i>₁₈ = -11.64, <i>P</i> < 0.003
Minimum record	-0.5 ± 1.9	-3.8 – 3.7	-3.6 ± 0.9	-4.8 – -1.5	---	---	<i>t</i>₁₈ = 8.29, <i>P</i> < 0.003
Late den season							
Natal den cavity							
Daily minimum	14.8 ± 3.8	12.6 – 18.7	11.2 ± 4.3	8.5 – 13.8	3.6 ± 1.4	1.3 – 6.6	<i>t</i>₁₄ = 8.18, <i>P</i> < 0.003
Daily mean	16.5 ± 3.9	13.0 – 20.3	17.2 ± 4.8	14.7 – 20.8	-0.8 ± 1.8	-3.6 – 0.1	<i>t</i> ₁₄ = -3.87, <i>P</i> = 0.001
Daily maximum	18.5 ± 4.0	13.6 – 22.2	29.5 ± 6.6	18.8 – 38.7	-11.0 ± 4.2	-25.1 – 2.0	<i>t</i>₁₄ = -7.65, <i>P</i> < 0.003
Minimum record	7.2 ± 2.2	3.0 – 10.1	3.2 ± 2.5	0.1 – 10.8	---	---	<i>t</i>₁₄ = 4.40, <i>P</i> < 0.003
Maternal den cavity							
Daily minimum	13.2 ± 3.8	11.0 – 17.6	10.7 ± 4.0	9.6 – 13.3	2.6 ± 0.9	0.7 – 5.6	<i>t</i>₁₈ = 7.47, <i>P</i> < 0.003
Daily mean	15.8 ± 3.9	13.8 – 18.5	16.7 ± 4.5	14.8 – 19.5	-0.9 ± 1.2	-2.5 – 0.1	<i>t</i>₁₈ = -5.65, <i>P</i> = 0.003
Daily maximum	18.8 ± 4.3	15.5 – 22.7	29.2 ± 7.0	19.8 – 39.1	-10.3 ± 4.0	-19.0 – -1.1	<i>t</i>₁₈ = -8.12, <i>P</i> < 0.003
Minimum record	5.7 ± 1.9	2.1 – 9.8	2.5 ± 0.9	1.1 – 5.1	---	---	<i>t</i>₁₈ = 8.06, <i>P</i> < 0.003

Table 3. Summary of data associated with fisher den clusters (i.e., a group of reproductive den structures used by one female in a single year) in the southern Sierra Nevada. We located reproductive dens of 45 adult female fishers between 2008 and 2015; 81 of the attempted den opportunities were successful. Perimeters of den clusters were calculated using the convex hull approach for females using ≥ 3 dens in a season. We calculated the area of den clusters with ≥ 2 dens that included a buffer of 370 m (based on average distance moved between dens) to assess their potential for use in forest management. For comparison of spatial relevance with den clusters, we calculated 30% and 95% fixed-kernel annual home ranges. Mean distance to the nearest known active natal den was also calculated to indicate the distance potentially required between patches of potential fisher den habitat in forested landscapes.

Characteristics Related to Den Clusters	Mean (\pm SD)	Range	<i>n</i>
Number of structures per reproductive opportunity	3.4	1 - 6	81 successful den attempts
Mean number of moves per den opportunity	2.6	0 - 6	81 successful den attempts
Mean distance moved between dens	364 m (\pm 314)	0 – 1894 m	81 successful den attempts
Total distance between dens in a season	930 m (\pm 650)	0 – 2718 m	81 successful den attempts
Area within den cluster perimeter	10.5 ha (\pm 12.8)	0.1 – 61.8 ha	65 den clusters (with ≥ 3 dens)
Area within den cluster polygon with 370 m buffer	107.8 ha (\pm 44.3)	49.0 – 259.0 ha	76 den clusters (with ≥ 2 dens)
Area of 30% kernel annual HR	150.9 ha (\pm 91.6)	37.9 – 520.7 ha	91 den attempts
Area of 95% kernel annual HR	1,469.3 ha (\pm 807.3)	458.8 – 5,840.7 ha	91 den attempts
Distance to nearest (known) active natal den	2,597 m (\pm 1216)	980 – 7,570 m	84 den attempts

Figure 1. The Kings River study area was located in the southwestern portion of the Sierra National Forest (a). Female fishers were captured and tracked to reproductive dens near Shaver Lake, California in elevations ranging from around 1,000 to 2,400 m (b).

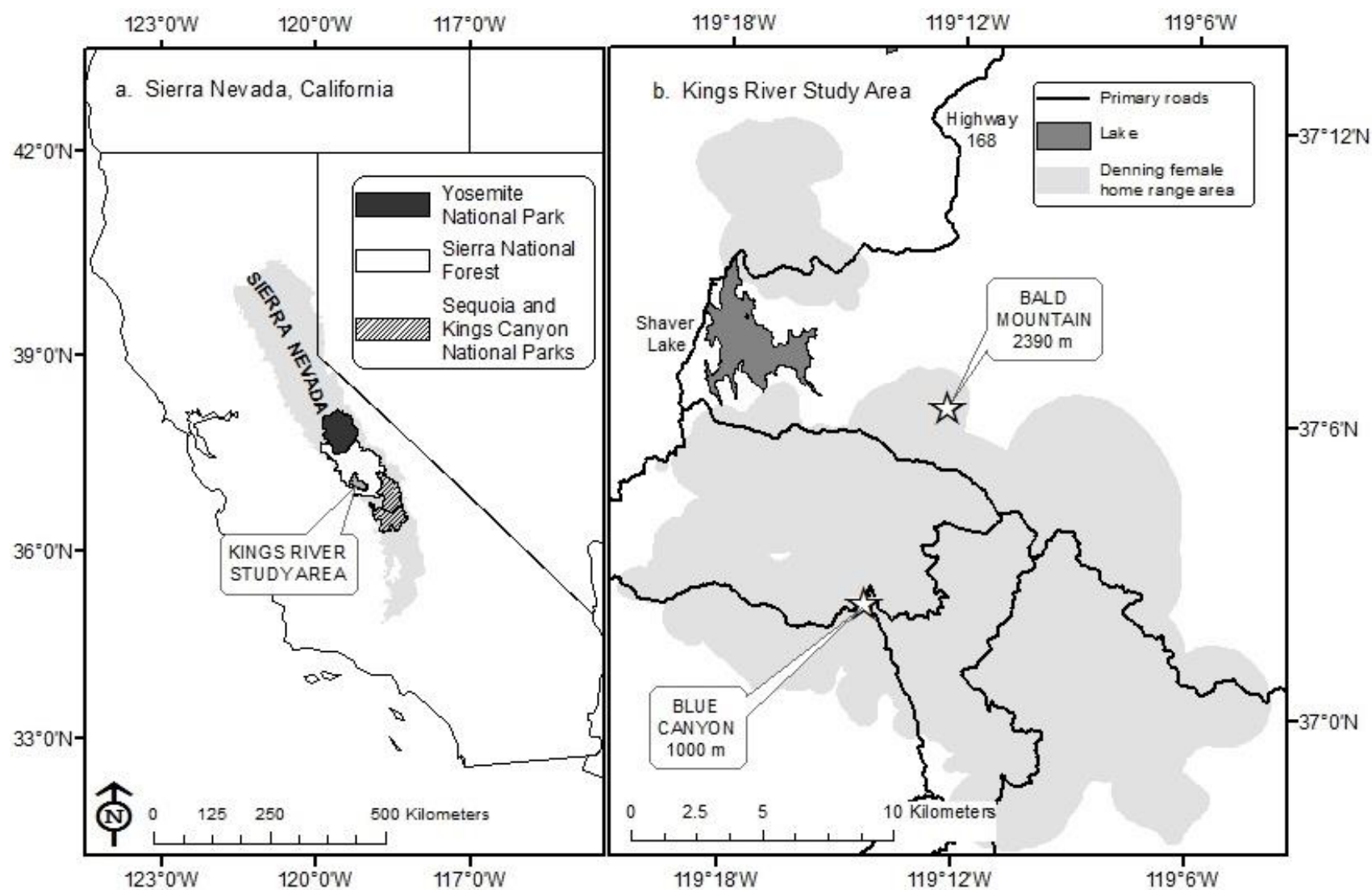


Figure 2. Examples of physical measurements collected at tree cavities used as fisher den microsites. Photos (a, b) show cavities at which functional entrances (opening used by female fisher) were the same as actual entrances (physical opening), thus vertical and horizontal measures were equivalent; entrances to natal den cavities and some maternal den cavities were often comparable in size to a human fist (c). In other cases, measures of functional openings were smaller than actual openings (d); this often occurred when the actual entrance was a long vertical scar, but only a smaller section (functional opening) was accessible by the female fisher as in (d). Floor dimensions in deep cavities (e) were often measured by taking a photo or video of the floor with a ruler for scale to assess the widest section and a perpendicular width. External temperature loggers (f) were attached to a metal bracket and secured to the tree; internal loggers were hung inside the cavity by a strong thin cord which was secured outside the cavity.

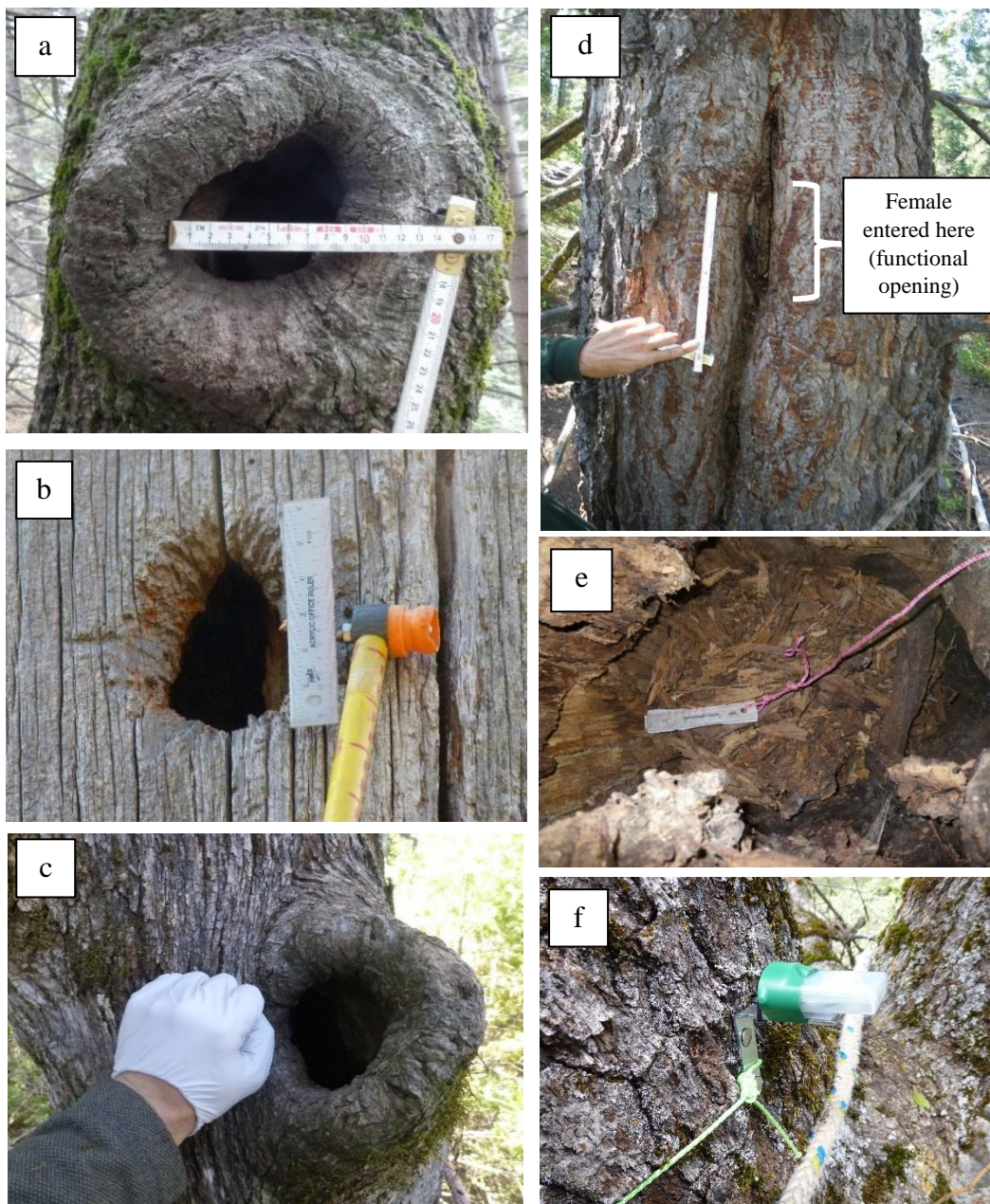


Figure 3. Example photos of female fishers and kits at reproductive dens. Photos (a, b) show the small size of a natal den cavity entrance (from a primary excavator, likely pileated woodpecker) in a conifer snag relative to the size of an adult female fisher. Photo (c) shows the small size of a fisher kit being moved from a natal den (entrance via a broken limb) in the early den season, while (d) demonstrates the challenge for a female transporting a large kit late in the den season. Photo (e) shows 2 young kits partially covered by a lining of wood chips in a natal den cavity.

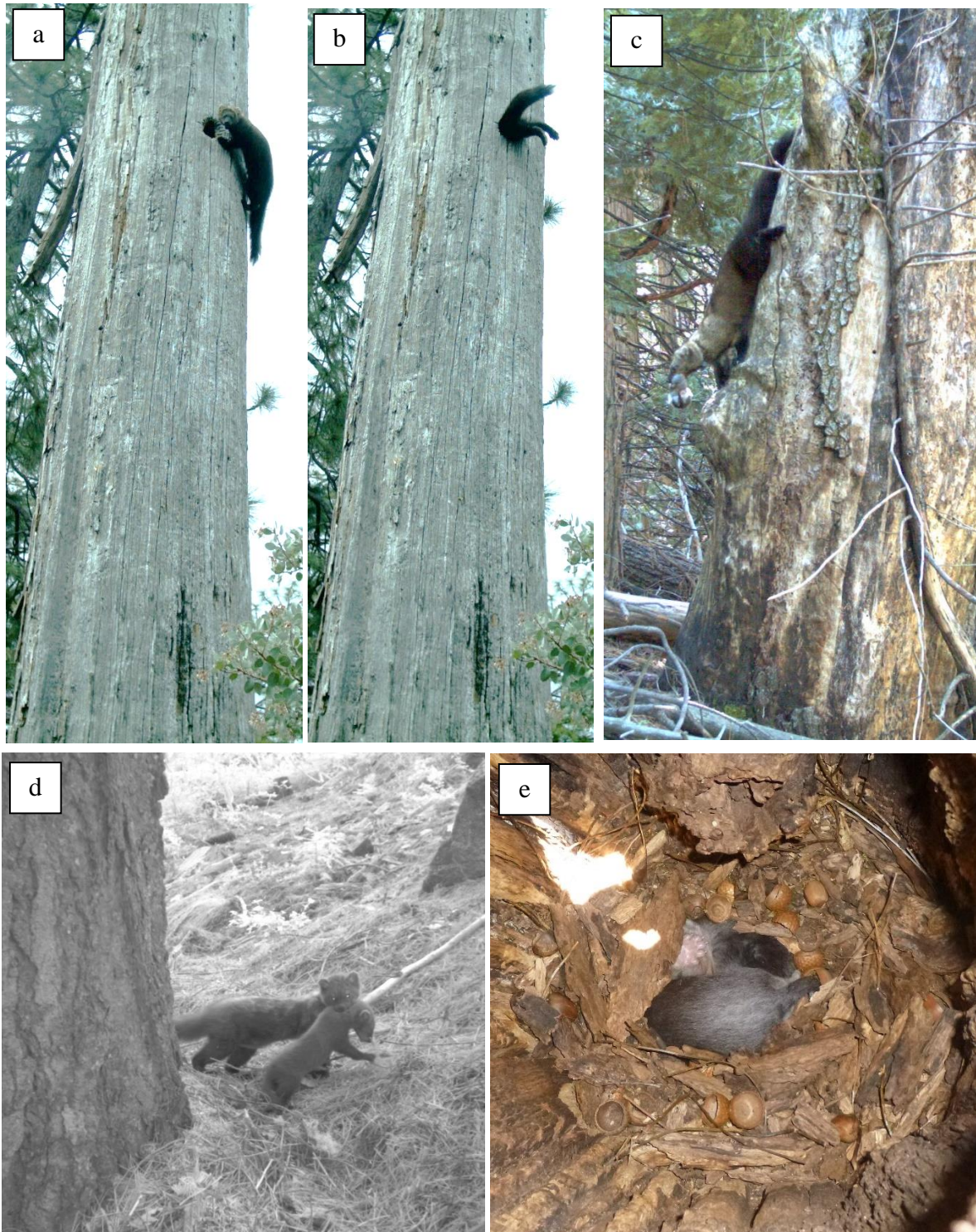


Figure 4. Temperature profiles inside and outside natal and maternal dens. Panel (a) summarizes daily minimum and mean temperature data from inside and outside cavities across previously occupied fisher dens (15 natal and 19 maternal combined) during the 2013 den season. Panel (b) highlights temperatures and buffering capacity of one natal and one maternal den during some of the coldest days monitored; both den structures were live California black oaks with similar diameter at breast height measures (natal 69 cm, maternal 72 cm).

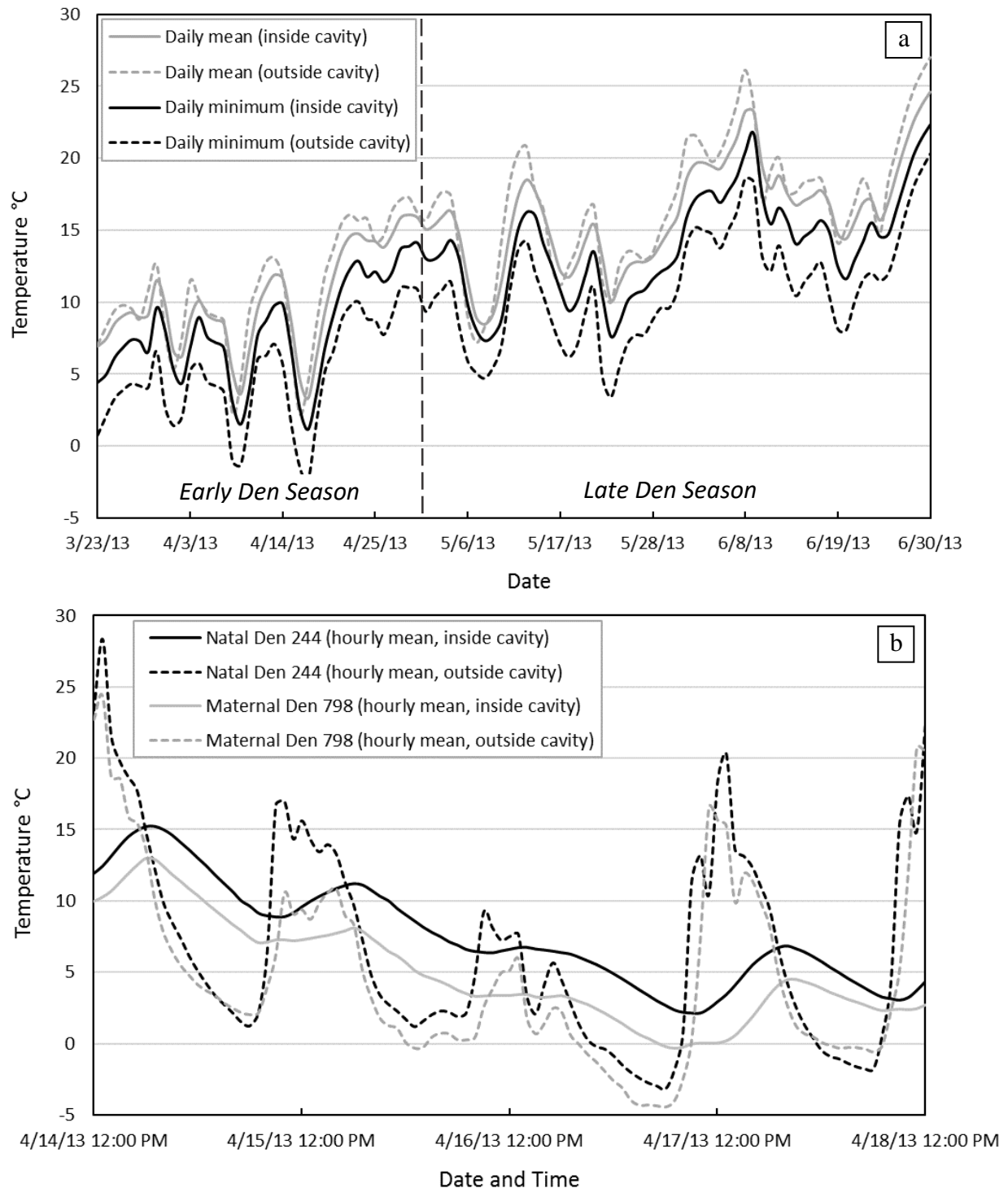


Figure 5. Temperature data loggers deployed inside and outside cavities of previously used fisher natal and maternal dens exhibited differences in thermal buffering capacity. As might be expected, the proportion of hours that fell below a cold threshold of 5° C was greater outside than inside both natal and maternal den cavities. However, the proportion of hours with temperatures below 5° C was also smaller inside natal den cavities compared to inside maternal den cavities. The proportion of cold temperatures recorded outside natal dens did not differ from those at maternal dens.

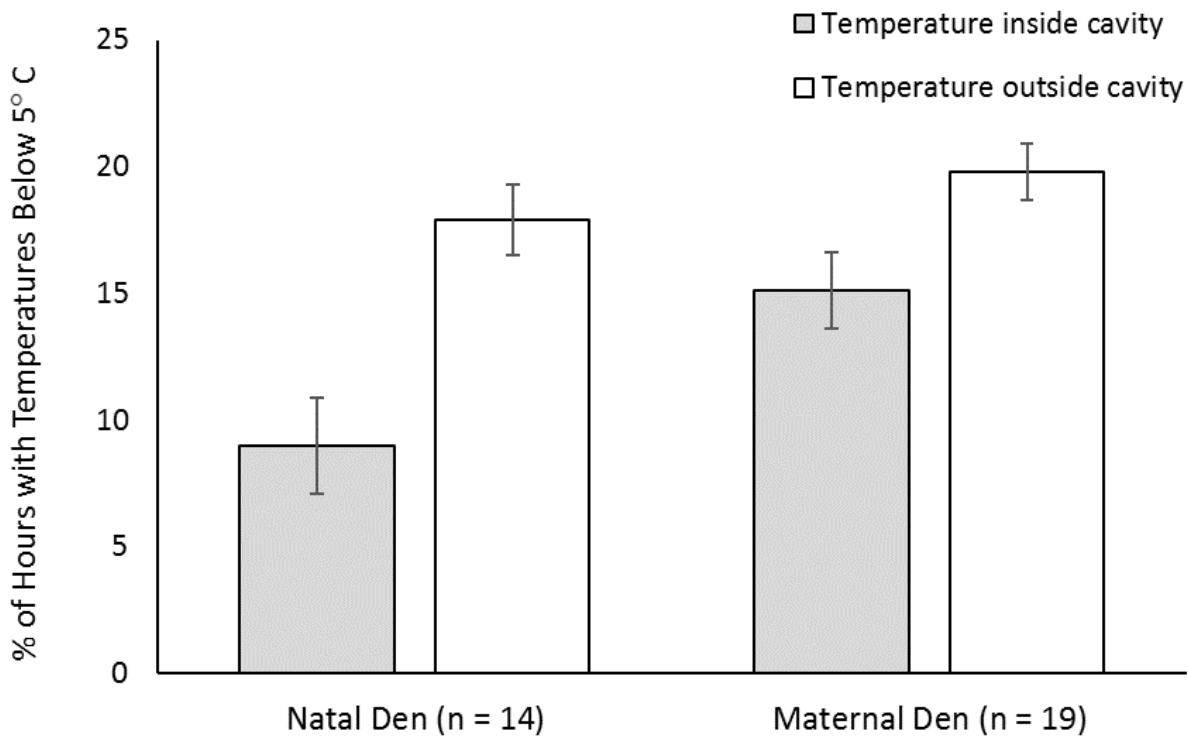


Figure 6. Distribution of the number of den structures used by individual female fishers during a single reproductive season in the southern Sierra Nevada. Counts were obtained from 39 female fishers over 81 successful den opportunities that were monitored for the full den season in the Kings River study area over 8 den seasons (2008 – 2015).

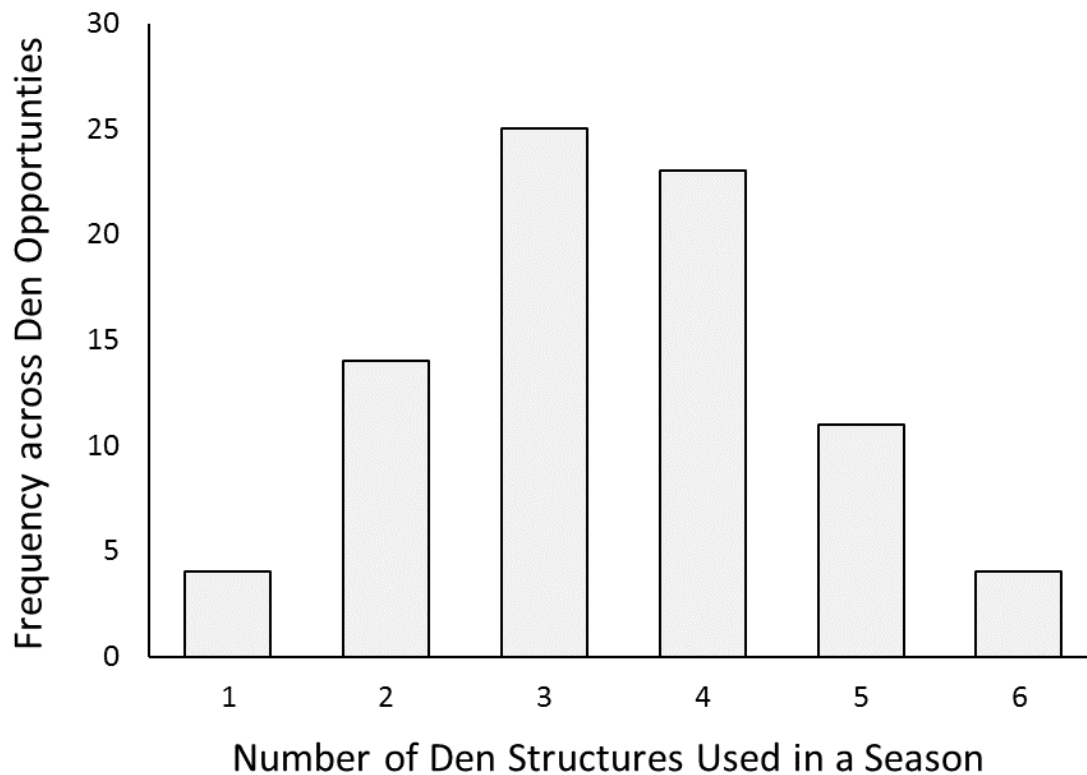
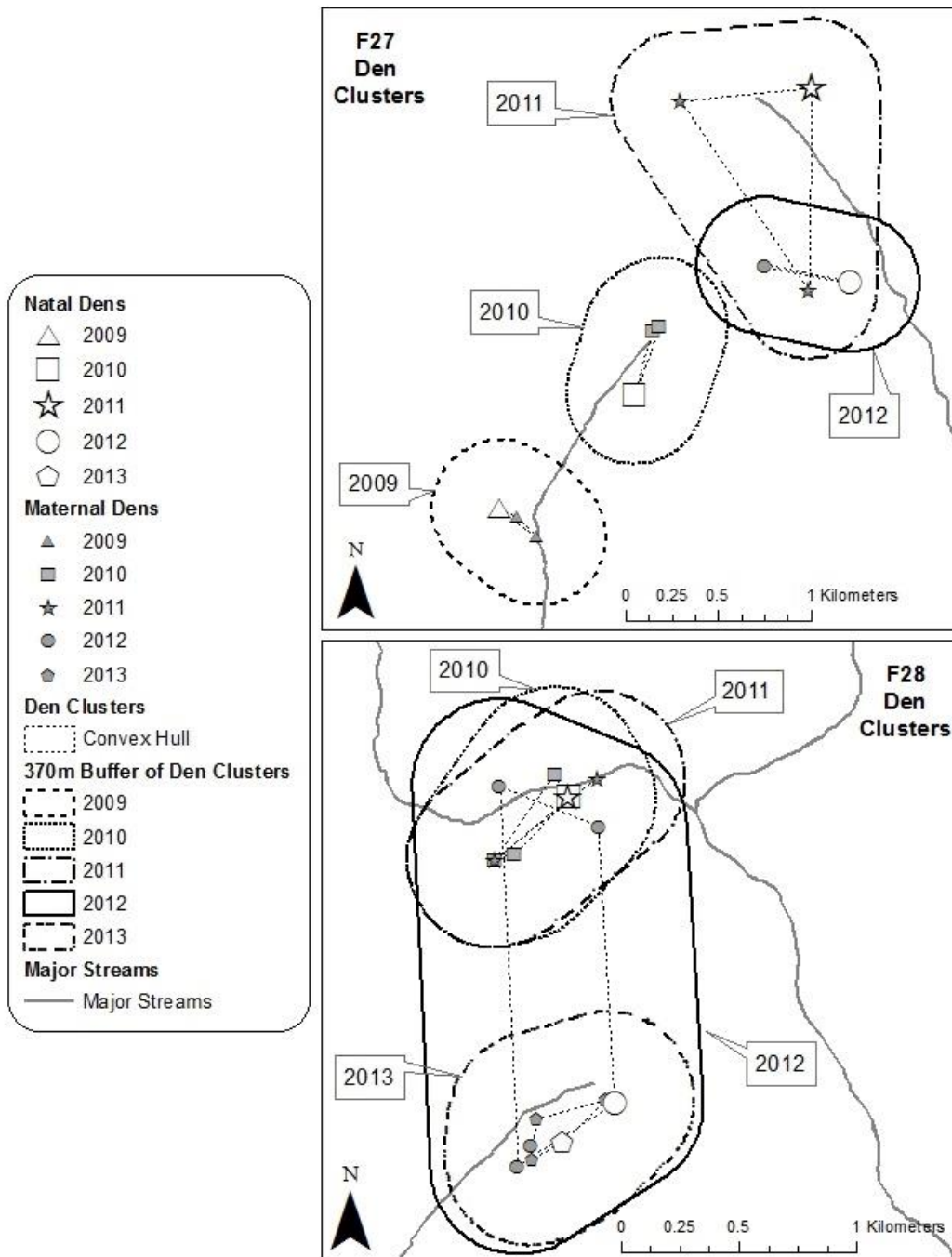
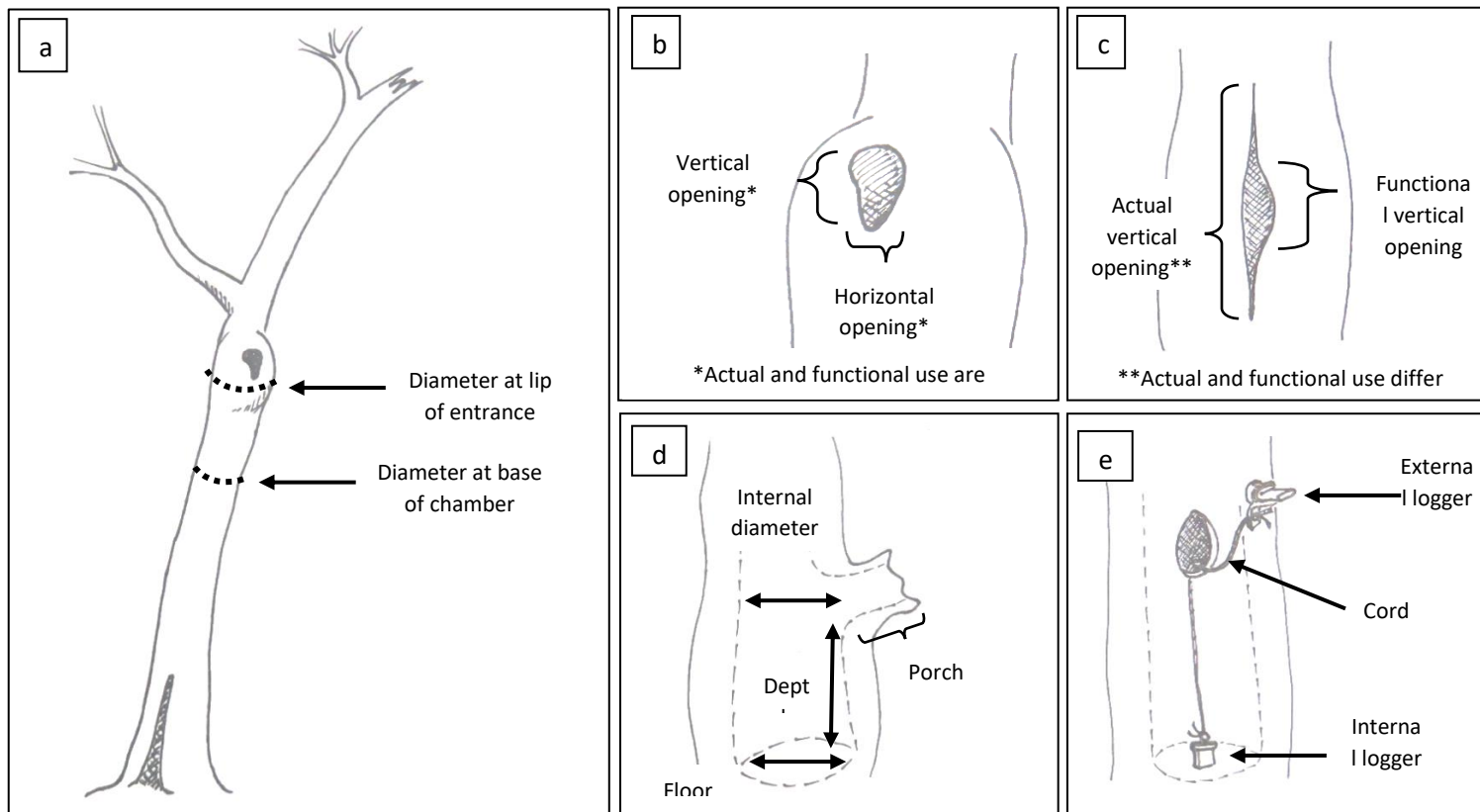


Figure 7. Examples of den clusters used by 2 reproductive female fishers (F27, F28), each of which reproduced in 4 consecutive years in the Kings River study area. F27 used 3 dens with similarly compact, but not overlapping, spatial patterns in 2009 and 2010. In 2011, F27 moved to a new drainage and used 3 widely spaced dens; in 2012, F27 used 2 different dens in an area that overlapped with the 2011 cluster. F28 used 4 dens in 2010 and 3 dens in 2011; her clusters overlapped extensively in these years, and included reuse of 1 natal and 1 maternal den structure. In 2012, her first 3 dens were in a new drainage to the south, then she moved to 2 dens near her 2010 and 2011 den clusters in the northern drainage, resulting in a large cluster. In 2013, all 4 of F28's den structures were in the southern drainage.



Appendix A. Diagrams of measurements collected at tree cavities used by female fishers as den microsites in the southern Sierra Nevada. Tree diameter was measured around the bole at the lower lip of the cavity entrance and at the location of the cavity floor (a). Measurements at the cavity entrance included horizontal and vertical measurements (b). In some cases, the functional opening used by the fisher was equivalent to the actual opening (b); in other cases, the functional opening was smaller than the actual physical cavity entrance on the tree (c). Cavity porch, depth, floor, and interior diameter measures were collected as in (d); when feasible, perpendicular measures were collected for the interior diameter and floor, along with floor shape, litter type, and litter depth. Temperature loggers were deployed as shown in (e). The external logger was attached to a metal L-shaped bracket using a plastic zip-tie and electrical tape; the bracket was attached to the east side of the tree with the logger facing upwards. The internal logger was hung inside the cavity by a length of polyethylene throwline (or thin copper wire depending on characteristics of the cavity); the free end of the cord or wire was attached to the metal bracket or an additional metal screw as needed for security and later retrieval (e).



Appendix B. Summary of monthly temperature data for months that overlap with the fisher denning season (March – June) from a weather station located in the northwestern portion of our study area, just southeast of Shaver Lake, California. Data were obtained from the National Centers for Environmental Information (<https://www.ncdc.noaa.gov/cdo-web/>) using the on-line search tool and selecting the global summary of the month dataset. We present data averaged across all years in which we located reproductive dens of female fishers (2008 – 2015) in the upper portion of the table; for comparison, we show data only from the year (2013) when we deployed temperature loggers at tree cavities previously used as fisher den microsites in the lower half of the table. Mean elevation of all reproductive dens (~1,500 m) located during our study was slightly lower than the elevation of the Shaver Lake weather station (~1,750 m); however, we did document fisher dens at and above the elevation of the weather station.

Month	Temperature (°C)					Number of Days	
	Mean	Mean Minimum	Mean Maximum	Extreme Minimum	Extreme Maximum	Below 0.0°C	Above 21.1°C
Mean values across years (2008 – 2015)							
March	4.4 ± 1.5	-3.4 ± 1.4	12.2 ± 1.8	-9.4 ± 3.3	20.1 ± 1.9	28.1 ± 3.2	0.6 ± 0.9
April	5.8 ± 1.3	-2.0 ± 1.1	13.6 ± 1.4	-9.3 ± 1.7	22.5 ± 1.8	23.5 ± 4.0	2.1 ± 1.6
May	9.2 ± 2.1	1.3 ± 1.6	17.1 ± 2.8	-3.3 ± 2.3	25.9 ± 2.5	11.6 ± 6.8	9.0 ± 5.6
June	14.2 ± 1.6	5.1 ± 1.1	23.3 ± 2.3	-0.5 ± 1.5	31.3 ± 1.4	1.1 ± 1.1	20.5 ± 4.9
Mean values during 2013							
March	5.6	-1.9	13.2	-6.1	21.7	28.0	2.0
April	7.6	-0.3	15.5	-8.3	23.3	17.0	3.0
May	10.2	2.0	18.4	-2.8	26.7	8.0	11.0
June	14.2	5.1	23.3	-0.5	31.3	1.1	20.5

Appendix C. Distribution of the coldest hour of the day recorded by temperature loggers positioned inside (dark triangles) and outside (hollow triangles) natal dens ($n = 15$) during the early den season (late March – April). The coldest hour was identified for each day at each den, then times were averaged across all natal dens; in cases where the same cold temperature occurred across multiple hours, we selected the latest time to represent the day. Notably, the coldest hours inside the natal den cavities were nearly always later than the coldest ambient temperature; the mean coldest hour inside cavities was 9:48 (± 3 hours 33 minutes SD; range 6:44 – 22:21) while the mean coldest hour outside cavity was 7:14 (± 4 hours 40 minutes SD; range 3:00 – 22:42). This thermal pattern corresponds with field observations that female fishers are generally found at dens in the morning hours during the early den season, possibly to provide additional warmth for young kits during the coldest time of the day.

