Forest Ecology and Management 440 (2019) 131–146

Contents lists available at ScienceDirect

Forest Ecology and Management

journal homepage: www.elsevier.com/locate/foreco

Microsites and structures used by fishers (*Pekania pennanti*) in the southern Sierra Nevada: A comparison of forest elements used for daily resting relative to reproduction

Rebecca E. Green[a,c,*], Kathryn L. Purcell[a], Craig M. Thompson[a,b], Douglas A. Kelt[c], Heiko U. Wittmer[d]

[a] USDA Forest Service, Pacific Southwest Research Station, 2081 E Sierra Ave, Fresno, CA 93710, United States
[b] USDA Forest Service, Region 1, 24 Fort Missoula, Missoula, MT 59804, United States
[c] Graduate Group in Ecology and Department of Wildlife, Fish, and Conservation Biology, 1081 Academic Surge, University of California, One Shields Ave, Davis, CA 95616, United States
[d] School of Biological Sciences, Victoria University of Wellington, PO Box 600, Wellington 6140, New Zealand

A R T I C L E I N F O

Keywords:
Den
Fisher
Habitat
Pekania pennanti
Reproduction
Rest
Sierra Nevada

A B S T R A C T

Many wildlife species rely on unique features of trees during daily activities and fundamental parts of their life cycle. The fisher (*Pekania pennanti*) is a forest-dwelling carnivore of conservation concern in western North America that uses unique habitat elements as refuges during resting bouts and for reproduction. Prior to this study, little was known about the fine-scale habitat used during reproduction at the southernmost extent of the fisher's range. Between 2007 and 2015, we attached radio-collars to 55 male and 72 female fishers in the southern Sierra Nevada and documented resting locations of males on 216 occasions (196 structures) and females on 824 occasions (737 structures). Beginning in 2008, we also monitored females over 8 reproductive seasons, confirming 45 females at dens and documenting 95 natal dens (83 structures) and 206 maternal dens (192 structures). We established 3 comparisons to guide our assessment of fine-scale habitat: resting males versus resting females, natal dens versus maternal dens, and resting fishers (both sexes) versus denning fishers (all dens). We expected the need for physical security and thermal protection in combination with morphology, predation risk, and aspects of reproductive ecology would influence patterns of use. Both sexes used a variety of microsites for resting, but females selected tree cavities most frequently (47%) while males used branch platforms most often (39%). For resting structures, live conifers were used most often by both sexes (males 44%, females 34%), but live hardwoods (males 16%, females 28%) and conifer snags (males 16%, females 22%) were also important. Comparing natal and maternal dens, we found that cavity microsites used early in the den season tended to be higher than those used later, and large live hardwoods comprised roughly half of all natal (46%) and maternal (51%) den structures. For resting versus denning, we found that large diameter hardwoods were an important source of cavities for both activities, live conifers used for denning were larger than those used for resting, and den structures tended to be on steeper slopes than rest structures. White fir (*Abies concolor*), California black oak (*Quercus kelloggii*), and ponderosa pine (*Pinus ponderosa*) were selected most often by both sexes for resting. In contrast, denning females relied on California black oak (55%), but also used white fir (24%) and incense cedar (*Calocedrus decurrens*; 12%). As noted in studies further north, our findings highlight the value of large trees with decay to support fisher reproduction and daily refugia.

1. Introduction

Many wildlife species rely on habitat elements (e.g., ground burrows, rock outcrops, hollow logs) as refuges during daily resting bouts and as places of safety to rear young (Ruggiero et al., 1998; Lawton et al., 2006; Lesmeister et al., 2008; Ross et al., 2010). Forest-dwelling species often rely on unique features of trees (e.g., cavities, basal hollows) for shelter during such resting and reproductive activities (Hankerson et al., 2007; Lutermann et al., 2010; Cockle et al., 2011a; Clement and Castleberry, 2013). Selection of microsites by wildlife may

* Corresponding author at: USDA Forest Service, Pacific Southwest Research Station, 2081 E Sierra Ave, Fresno, CA 93710, United States.
E-mail address: rebeccagreen@fs.fed.us (R.E. Green).

https://doi.org/10.1016/j.foreco.2019.02.042
Received 6 September 2018; Received in revised form 22 February 2019; Accepted 24 February 2019
0378-1127/ Published by Elsevier B.V.

be influenced by qualities such as the capacity for physical security and thermal protection (Taylor and Buskirk, 1994; Willis and Brigham, 2005; Fontaine et al., 2007; Joyce et al., 2017). Fine-scale habitat features may also confer other benefits to animals such as places to cache food or interact with con-specifics (Korpimäki, 1987; Willis and Brigham, 2007). Some wildlife species have the capacity to construct their own protected microsites in trees, while others rely on primary excavators, nest builders, or general processes of tree growth and decay to form suitable refuges (Martin and Eadie, 1999; Cockle et al., 2012; Bunnell, 2013). Habitat elements of high value to forest-dwelling wildlife often take many years and multiple processes to develop (e.g., trees with large cavities), thus they have the potential to become limiting factors, especially for species that do not create their own refuges (e.g., secondary cavity users; Cornelius et al., 2008; Cockle et al., 2010; Cockle et al., 2011b). Determining the characteristics of trees and other structures that contribute to species meeting basic life history requirements is important for conservation plans (Trousdale and Beckett, 2005; de la Parra-Martínez et al., 2015).

The fisher (*Pekania pennanti*) is a forest-dwelling mesocarnivore whose range in North America has been reduced and fragmented largely as a result of fur trapping and loss of mature forest habitat (Gibilisco, 1994; Lewis and Zielinski, 1996; Laliberte and Ripple, 2004). This species is of conservation concern in California, Oregon, and Washington, with particular concern for fishers living at the southernmost extent of the range in the Sierra Nevada due to issues such as geographic isolation and low genetic diversity (Wisely et al., 2004; Zielinski et al., 2005; Lofroth et al., 2010). Fishers are associated with forest attributes that take time to develop, including large decadent trees used for resting throughout the year and denning in spring (Weir et al., 2012; Aubry et al., 2018). Previous studies indicate that fishers use trees with unique microsites (e.g., tree cavities, witches' brooms) during daily resting activities (Zielinski et al., 2004a; Purcell et al., 2009; Gess et al., 2013; Aubry et al., 2018). In contrast, reproductive dens have consistently been documented in large diameter trees with hollows (Paragi et al., 1996; Aubry and Raley, 2006; Weir et al., 2012).

Fishers do not create their own rest or den microsites; instead, they rely on other species and ecological processes to form features with desirable criteria such as physical security and thermal protection. Although some types of habitat elements may be preferred, local abundance may constrain choice such that proximity or availability of less optimal habitat elements may override other qualities in some situations. Previous research suggests that individual fishers may fine-tune selection of habitat elements to accommodate their activity (e.g., resting, denning) or prevailing weather conditions, but that factors such as morphology, mortality risks, and reproductive ecology may also play an influential role (Green, 2017; Joyce et al., 2017). Fishers are sexually dimorphic, with juvenile males generally exceeding adult females in size and weight by the time they near independence (approximately 6–8 months of age; Green, Unpublished Results). Once males have reached adulthood (≥ 2 years of age), they can weigh twice as much as females and have notably broader heads (Powell, 1993; Powell et al., 2003). Predation by mammalian carnivores larger than fishers is the most common cause of mortality in the southern Sierra Nevada, with added impacts from disease and toxicants associated with illegal marijuana grows (Wengart et al., 2014; Gabriel et al., 2015). Finally, fisher reproductive ecology is unique in ways that might influence den site selection. Females can mate for the first time at 1 year, but do not give birth until at least 2 years of age after an extended period of delayed implantation (Powell et al., 2003). Annual reproductive output is low, with females giving birth to small litters once a year in late winter or early spring, and mating occurring during a brief period after parturition (Powell et al., 2003; Green et al., 2018).

Sexual dimorphism in adult fishers is notable and indicates potential differences in the need for physical protection and thermal security at fine-scales; however, only a few studies have compared habitat use of males and females at this spatial scale (Kilpatrick and Rego, 1994; Powell et al., 2003; Zielinski et al., 2004a). Wengart et al. (2014) found that smaller-bodied female fishers were killed by a wider range of predators (i.e., mountain lion (*Puma concolor*), bobcat (*Lynx rufus*), and coyote (*Canis latrans*)) when compared with males (primarily mountain lions). This difference in predation pressure may compel females to seek out resting locations with greater physical security than males. The "weasel" body shape (long, thin) is associated with increased energetic costs due to a high surface-area-to-volume ratio and species with this body shape can conserve energy during cold conditions by using insulated microsites (Brown and Lasiewski, 1972; Joyce et al., 2017). Male fishers should have greater resiliency to low temperatures due to their large body size, thus may have less need for microsites with robust insulation than females. Although not thoroughly studied, the opposite pattern may be true in hot conditions when larger-bodied males may be more susceptible to heat-stress than females. Fishers have been known to select cool, moist locations during hot conditions, thus habitat elements that provide cool refugia may be of special value to males (Zielinski et al., 2004a; Aubry et al., 2013). In summary, we expect the larger body size of males to be associated with lower predation risk and lower susceptibility to cold temperatures (but higher risk of heat-stress in hot conditions) and restrict access to small spaces. In contrast, we expect the smaller body size of females to be associated with greater vulnerability to predation, increased susceptibility to cold temperatures (but perhaps less bothered by hot conditions) and allow access to a greater range of microsites than males.

We have identified reasons that female fishers may choose to rest in locations with greater physical and thermal protection (from cold temperatures) than males. We suspect these reasons will be even more compelling for females at reproductive dens to meet the needs of kits (Paragi et al., 1996) and offset energetic costs of reproduction (Powell and Leonard, 1983). As in other geographic areas, we expect female fishers in the southern Sierra Nevada to find protected den microsites in cavities of large decadent trees, particularly hardwoods (e.g., Weir et al., 2012). Relative to resting locations, we expect denning females to select structures of sufficient size and decay to contain fisher-sized cavities, but still have suitable physical and insulative properties. We also expect that female criteria for selecting den locations may change over the season to accommodate increasing size and mobility of kits (Wynne and Sherburne, 1984; Powell et al., 1997). Specifically, entrances that are higher off the ground may be preferred during and soon after parturition (natal dens) to increase physical safety and solar exposure (i.e., to warm kits), while lower microsites may be chosen later in the season (maternal dens) when kits are larger, more difficult to transport, and at risk of falling while learning to climb. Females may also use cavities with smaller more secure entrances at natal dens compared to maternal dens to protect kits by excluding males during the mating period. A documented case of a male killing kits at an artificial den box indicates this is a valid concern (Davis, 2018).

To maintain a supply of structures that can meet the potentially variable daily resting and seasonal reproductive needs of a fisher population, forest managers need to know which trees within the local pool of structures are suitable and whether different types of structures fulfill different needs. Information from studies in other geographic areas can provide background on general patterns of fine-scale habitat use by fishers (Aubry et al., 2013). However, because individual tree species vary in their distribution and susceptibility to decay, these patterns may not provide enough information for local management plans. In the southern Sierra Nevada where conditions are generally hotter and drier than other parts of the range, available tree species and growing conditions differ from those further north and east. Thus, local or regional data may be necessary to identify the trees most likely to yield features that support critical life history requirements for fishers (e.g., tree cavities for reproduction). Determining whether the fine-scale habitat needs of fishers overlap or are specialized by sex or activity is also important to effectively manage habitat for fishers (Appendix A). For example, can male and female fishers use the same types of structures for resting or do their needs differ substantially? Are some trees more suitable for natal dens (early season) compared to maternal dens (later den season), and vice versa? And how similar (or dissimilar) are structures used for denning compared to those used for resting? The answers to these questions are interesting from a biological perspective, but also of value in clarifying the diversity of structures needed to support a fisher population and whether certain types of trees can serve multiple purposes.

Although previous studies have described fine-scale resting habitat for fishers, the labor-intensive nature of the field work has constrained data collection to modest time frames (often < 2 years) or a relatively few individuals (often < 20; Zielinski et al., 2004a; Purcell et al., 2009; Gess et al., 2013). Data for fisher reproductive dens are also still somewhat limited and restricted to certain portions of the fisher's distribution (Powell et al., 1997; Weir et al., 2012; Erb et al., 2015). Prior to the initiation of this study, only a handful of reproductive dens had ever been located in the Sierra Nevada (Grinnell et al., 1937; Truex et al., 1998). Accordingly, there have been few opportunities to explore similarities and differences in the types of microsites and structures used by fishers for resting relative to those used for reproduction on a local population. Using data from a long-term study of fisher ecology in the southern Sierra Nevada, our objectives were to (1) investigate the degree to which male and female fishers differ in their use of fine-scale resting habitat, (2) identify any notable differences in the fine-scale habitat used by reproductive female fishers at natal and maternal dens (i.e., early versus later in the den season), and (3) summarize and contrast the characteristics of microsites and structures used for resting and denning. Moreover, we explore the role that individual tree species may play in providing fishers with suitable fine-scale habitat to meet critical life history needs in the southernmost portion of this species' range. We consider our findings relative to expected variation in the need for physical and thermal security within a local population and the role that morphology, predation risk, and reproductive ecology may play in fine-scale habitat use by fishers.

2. Materials and methods

2.1. 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 slope of the southern Sierra Nevada (Fig. 1). We focused live trapping efforts at elevations from 1000 to 2000 m. Precipitation generally occurs in fall (as rain) and winter (as snow in elevations ≥ 1500 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 (> 1500 m) and a mixture of hardwood and conifer species at lower elevations (< 1500 m). Available hardwoods included California black oak (*Quercus kelloggii*), Canyon live oak (*Q. chrysolepis*), white alder (*Alnus rhombifolia*), and big leaf maple (*Acer macrophyllum*). Coniferous tree species in the area included white fir (*Abies concolor*), incense cedar (*Calocedrus decurrens*), ponderosa pine (*Pinus ponderosa*), sugar pine (*P. lambertiana*), and Jeffrey pine (*P. 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 in the area have included timber harvest, prescribed fire, and urban development, although areas of mature forest and patches of large remnant trees were retained. Fire suppression has led to increases in shade-tolerant species (e.g., white fir, incense cedar), tree densification, and increased understory fuels (Fites-Kaufman et al., 2007).

2.2. Animal handling

To facilitate radio-collar attachment, we trapped, anesthetized, and handled fishers using established protocols that maintained animal and human safety. We outline the basic methods here, but further details are described in Green (2017) and Green et al. (2018). We concentrated live-trapping efforts for fishers in the autumn and winter (October through February). We caught fishers in live traps 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 inside the cubby, 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 (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 were processed at the site of capture after all traps were checked. Once sedated, fishers were fitted with Holohil radio-collars (model MI-2M, 31 g, Holohil Systems Ltd., Carp, Ontario, Canada) equipped with a handmade breakaway device. We did not attach collars to any juvenile fishers weighing less than 1.7 kg; individuals this small were still growing quickly in size, thus attaching a collar that would stay on but not become constricting was challenging. Holohil collars weighed < 2% of body weight. 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. (2018). Once anesthesia began to wear off, fishers were returned to the cubby, where they were held until fully recovered, then released. Capture and handling procedures were approved by the Institutional Animal Care and Use Committee of the University of California, Davis and met guidelines outlined by the American Society of Mammalogists (Sikes et al., 2016).

2.3. Location of fisher rest sites and reproductive dens

Field work was conducted year-round, with seasonal priorities for technicians largely corresponding with fisher reproductive ecology (March–June: denning, July–October: mobile kit rearing, November–February: kit independence). Although we put in greater effort to obtain locations of female fishers in spring to confirm dens, we did locate resting fishers of both sexes and all ages year-round as time allowed between other activities (e.g., spring den monitoring, summer vegetation measurement, winter trapping). During daily fisher monitoring efforts, we opportunistically located inactive radio-collared fishers using triangulation and homing techniques to identify structures used for resting (see Zielinski et al. (2004a) and Green et al. (2017) for details on techniques). From early March through June we focused telemetry efforts on inactive adult females in early morning hours to locate reproductive dens (Matthews et al., 2013; Green et al., 2017). When locating both rest and den structures, we typically used triangulation to assess the location of individual animals. Although our radio-collars did not have activity processors, inactive signals could be identified with practice. An animal was considered inactive if the signal

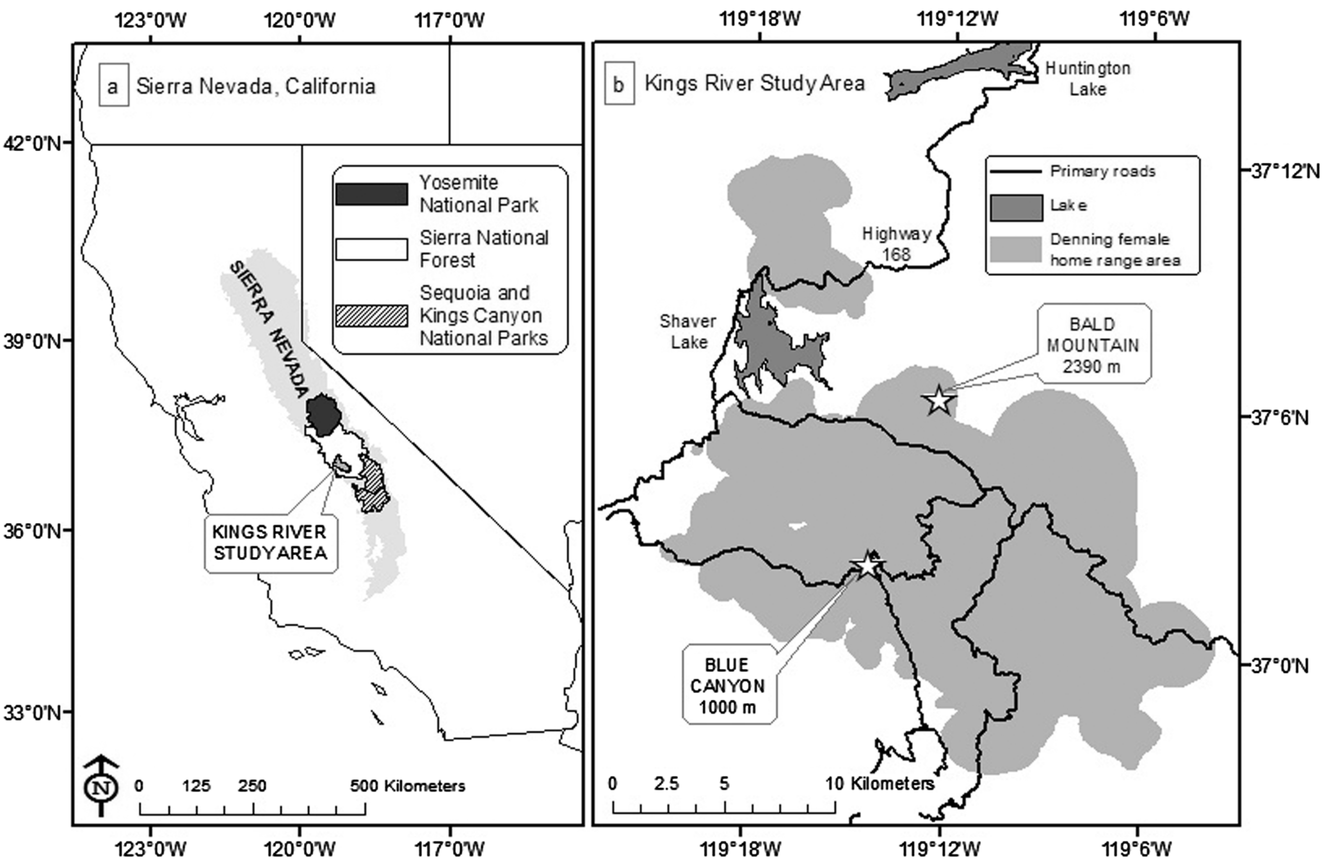


Fig. 1. Location of the Kings River study area (a) in the southwestern portion of the Sierra National Forest in the southern Sierra Nevada. (b) Combined home range area of all reproductive females over the course of the study (2007–2015).

from the transmitter remained consistent, with little to no fluctuation during the triangulation. If an inactive signal was obtained for ≥ 20 min, we then used homing techniques to locate the rest or den structure. 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 this analysis. Using these methods, we were confident that we located nearly all reproductive den structures used by radio-collared female fishers each year due to concentrated efforts; in contrast, we located a subset of the total number of rest structures used by male and female fishers each year. Although more effort was put towards locating females each spring (which resulted in locations of both dens and rest structures), the long-term nature of our project and year-round effort allowed us to identify a substantial number of rest sites associated with numerous individuals across seasons.

If an individual rest or potential den structure was identified, we attempted to locate the microsite using visual clues combined with the transmitter signal. In many cases, we were able to identify a single feature as the only apparent microsite consistent with the transmitter signal, and sometimes we observed the fisher. Although uncommon, den microsites occasionally showed evidence of repeated use (e.g., hairs at cavity entrance visible with binoculars, scratches in bark). Some den microsites were further verified during efforts to count offspring using additional techniques (e.g., tree climb; Green et al., 2017). If we could not identify a specific microsite with confidence, we recorded it as unknown. To distinguish unique habitat components, we adopted terms and descriptions used previously (Slauson and Zielinski, 2009; Matthews et al., 2013; Joyce et al., 2017) with modifications and additions based on our field experience (Table 1).

2.4. Microsites and structures used for resting and denning

Once a rest or reproductive den structure was located, we recorded the coordinates using a hand-held GPS unit, noted the location of the microsite (if identified), and described the structure (e.g., tree species, estimated tree diameter). To minimize disturbance, we returned on a later date when the site was not occupied to measure features of the microsite and structure. We recorded measurements at a large subset of rest locations (male and female) and at all reproductive dens (natal and maternal). If a microsite was identified, we assigned a 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). We grouped microsites into 6 categories: cavity in standing live tree or snag, cavity in log, platform associated with a branch or branches, platform created by broken trunk of tree ("broken top"), burrow, and interstitial space (i.e., protected area within or under a combination of logs, rocks, or vegetation on the ground). These microsite type categories were based on similarity of origin in creation (e.g., heart rot likely contributed to the formation of most cavities) and comparable function for fishers (e.g., enclosed spaces in cavities and burrows versus more exposed spaces in platforms). For descriptive purposes, we also identified subdivisions of microsite categories when possible (Appendix B). In the case of cavities and burrows, we considered microsite height to be the distance from the ground to the bottom of the entrance, although the resting fisher may have been lower inside a tree hollow or below ground level. As we rarely observed fishers at ground level locations, heights were typically estimated to be between 0 and 0.5 m depending on the characteristics of the structure (e.g., ground burrows were considered 0 m, while log cavities might vary from 0.2 to 0.5 m depending on characteristics of the log).

We categorized structures used for resting and denning by type

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., 2004; Weir et al., 2012; Joyce et al., 2017) 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 localization and maternal care during spring and early summer by adult female fishers with kits. Denning occurs in secluded places that are used repeatedly (i.e., a few consecutive days to > 1 month).
(Reproductive) 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. As the term "den" has been used more generally with other species, we suggest preceding with "reproductive" as needed to clarify function.
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) presumably used by a fisher for comfort, concealment, and/or protection from abiotic (e.g., temperature) and biotic elements (e.g., predators). Fishers do not appear to create microsites, these features are formed by natural processes and other species.
Rest Microsite	The specific fine-scale location of an inactive male or female fisher; this includes cavities and platforms (e.g., branch clusters, large branches, nests, broken tops) in live trees and snags as well as ground level features like hollows in logs, burrows in ground, rock, or snow, and interstitial spaces in 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, stump, ground cavern, 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 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 if 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 live trees and snags 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.
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	A place used by reproductive females with mobile kits after natal or maternal dens during mid- summer and early fall, but prior to kit independence in the fall. Kits may be left at sites while the female hunts.

(e.g., live hardwood, conifer snag), and determined slope (%) with a clinometer. We grouped structures into 6 categories: live hardwood, hardwood snag, live conifer, conifer snag, hollow log (hardwood or conifer), and other ground level structure (e.g., rock pile). As with microsites, these categories were based on source and function and can be readily distinguished by forest managers. For structures identified as live trees, snags, or logs, we identified tree species, measured diameter at breast height (dbh), and determined microsite height using a hypsometer. We recorded decay class for standing live trees and snags 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 are dead trees with increasing levels of decay.

2.5. Statistical analysis

To contrast microsites and structures used by fishers, we grouped data into 3 sets of comparisons: (1) rest locations of males versus those of females, (2) natal dens versus maternal dens of reproductive females, and (3) combined rest locations (males and females) versus combined reproductive 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 used all microsites or structures to calculate percent documented 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 dbh, slope, and elevation we applied 2-tailed *t*-tests. For some comparisons we transformed data to meet test assumptions (i.e., normal distribution, equal variance); we used log transformations with microsite height and structure dbh data and square root transformation for slope and elevation data. In a few comparisons of microsite height where data transformation was not effective, we compared groups with non-parametric Mann-Whitney U-tests. Where appropriate, within-den comparisons were between natal and maternal dens; however, to assess differences in microsite height, the time of selection within the den season was most important, so for that comparison we grouped dens as to whether they were selected early (March and April) or late (May and June), similar to Powell et al., (1997). We used a 1-tailed *t*-test to assess whether microsites (natural log-transformed data) were higher at natal and maternal dens selected early compared to maternal dens selected late. We assessed whether generalized microsite type categories (cavity, platform) differed between tree species using a chi-square test. We used analysis of variance (ANOVA) to evaluate differences in mean elevation at den structures across tree species. 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. Analyses were conducted in NCSS 12 (NCSS 2018) and R version 3.2.2 (R Core Development Team, 2015).

3. Results

3.1. General summary of fishers captured and locations (rest, den) identified

From June 2007 to December 2015 we captured and attached radio-collars to 55 male and 72 female fishers. We monitored fishers year-round through 2015 using ground telemetry, documenting males resting on 216 occasions (with 9.3% reuse of structures) and females resting on 824 occasions (with 10.4% reuse of structures; Table 2). Using time periods relevant to fisher ecology (denning: March–June; mobile kit rearing: July–October; independence: November–February), our locations of resting males were relatively well-distributed across seasons (36.2%, 38.6%, 25.2% respectively), but we found a higher

Table 2
Summary of microsite and structure types used for resting (male, female), denning (natal den, maternal den), and each activity combined (rest, den) by fishers in the southern Sierra Nevada 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 (n = microsites or structures)		% of All uses by denning fishers (n = microsites or structures)		% of All uses by fishers (n = microsites or structures)	
	Male	Female	Natal	Maternal	Rest Combined	Den Combined
Microsites						
Cavity – Tree	23.5% (42)	47.0% (320)	100.0% (83)	99.0% (190)	42.1% (352)	99.3% (265)
Cavity – Log	8.9% (16)	7.0% (48)	–	1.0% (2)	7.5% (63)	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	83	192	836	267
All documented uses	199	763	95	206	962	301
% Reuse	10.1%	10.7%	12.6%	14.0%	8.5%	11.3%
Structures						
Hardwood – Live	15.6% (39)	27.5% (203)	45.8% (38)	55.2% (101)	26.3% (239)	51.3% (137)
Hardwood – Snag	2.7% (5)	2.7% (20)	4.8% (4)	4.2% (7)	2.6% (24)	4.1% (11)
Conifer – Live	43.5% (81)	34.2% (252)	33.7% (28)	20.3% (36)	35.4% (322)	22.5% (60)
Conifer – Snag	16.1% (30)	21.6% (159)	15.7% (13)	26.6% (46)	20.1% (183)	21.3% (57)
Log	9.1% (17)	6.8% (50)	–	1.0% (2)	7.3% (66)	0.7% (2)
Other	12.9% (24)	7.2% (53)	–	–	8.4% (76)	–
Unique structures	196	737	83	192	910	267
All documented uses	216	824	95	206	1040	301
% Reuse	9.3%	10.4%	12.6%	14.0%	12.5%	11.3%

proportion of resting female locations during the denning period (52.7%, 29.4%, 18.0% respectively). We identified microsites of resting male fishers on 199 instances (with 10.1% repeat uses) and of resting females on 763 instances (with 10.7% repeat uses; Table 2).

We monitored 52 females as adults for ≥ 1 spring denning seasons, with 45 of these initiating natal dens in ≥ 1 year. Mean number of years for individual females initiating dens was 2.2 (range 1–7 years). Over 8 reproductive seasons (2008 through 2015) we located 95 natal dens (with 12.6% reuse of structures) and 206 maternal dens (with 14.0% repeat use of structures; Table 2). We documented microsites for denning female fishers on 301 occasions (95 natal dens, 206 maternal dens). All forest features used as microsites for resting and denning appeared to provide some degree of visual camouflage and physical security (Fig. 2). All cavity microsites occurred in boles of trees, with access points created by broken limbs, woodpecker holes, broken trunks, or cracks formed by damage (Fig. 2). 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

3.2.1. Comparison – fine-scale habitat used by resting male and female fishers

Males and females overlapped in the types of microsites used for resting, but they differed in their proportional use of these features ($X^2_4 = 33.84$, $P < 0.01$; interstitial spaces excluded due to low sample size). Males rested in platforms formed by branches most often, while females rested in tree cavities most frequently (Fig. 3, Table 4). Height of microsites used by males and females did not differ (Table 3), even if ground-level resting sites were excluded (males 11.6 m ± 6.5 SD, $n = 74$; females 10.8 m ± 7.0 SD, $n = 276$; $t_{348} = -0.85$, $P = 0.39$).

Male and female fishers used similar structure types for resting, but at different frequencies ($X^2_5 = 14.40$, $P = 0.01$; Table 4). Males used more live conifers than females; females used more live hardwoods and conifer snags than males (Fig. 4). Fishers used 11 different tree species for resting, but only 6 were used regularly (≥5 occasions) and the sexes differed in their use of these 6 species ($X^2_5 = 14.4$, $n = 840$, $P = 0.01$). Males used ponderosa pine more often than females, females used California black oak and incense cedar more than males, and both sexes used white fir at an equally high rate (Table 4). Despite proportional differences in use, white fir, ponderosa pine, and California black oak made up the bulk of all structures used by both sexes (Table 4).

Fishers rested in structures that were large in diameter (Table 3, Appendix C). Males rested in larger diameter conifer snags and logs than those used by females (mean ± SD, 127.2 cm ± 47.4 SD, 100.3 cm ± 28.5 SD respectively; $t_{189} = -4.20$, $P < 0.003$), but for other structure types the differences were not significant (Table 3). Both sexes rested in hardwoods with similar levels of decay; live trees with decay (class 2) were used most often (males 74.4%, females 68.8%), followed by live trees with little decay (class 1; 9.3%, 18.1%), and intact snags (class 3; 7.0%, 6.0%). Conifers used by males and females had a wider range of decay, most frequently in live trees with little decay (class 1; 43.6% and 33.1% respectively), followed by live trees with more decay (class 2; 25.5% and 24.6% respectively), and the remainder classified as snags with more extensive decay (including minor peaks around class 6; 10.0% and 15.5% respectively). Both sexes rested on similarly steep slopes. Males rested at slightly higher elevations than females (male mean 1602 ± 302 SD, range 1039–2555 m versus female mean 1524 ± 232 SD, range 965–2227 m; $t_{255.3} = -3.15$, $P = 0.002$).

3.2.2. Comparison – fine-scale habitat used by denning females early and late in the season

All natal den microsites and nearly all maternal den microsites (99.0%; 2 late season exceptions in log cavities), were in tree cavities (Fig. 3, Table 2). Den microsites located early in the season (including natal and maternal dens selected in March and April) were higher than those found later (May and June; $t_{259} = 3.92$, $P < 0.01$). Height of den microsites 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 conifer snags, live hardwoods, hardwood snags, then logs.

Although the types of structures used by females as natal and maternal dens overlapped, proportion of use differed ($X^2_3 = 8.14$, $P = 0.04$, Table 2; excluding logs due to small sample size). Natal and maternal dens both occurred most often in live hardwoods; for natal dens, the

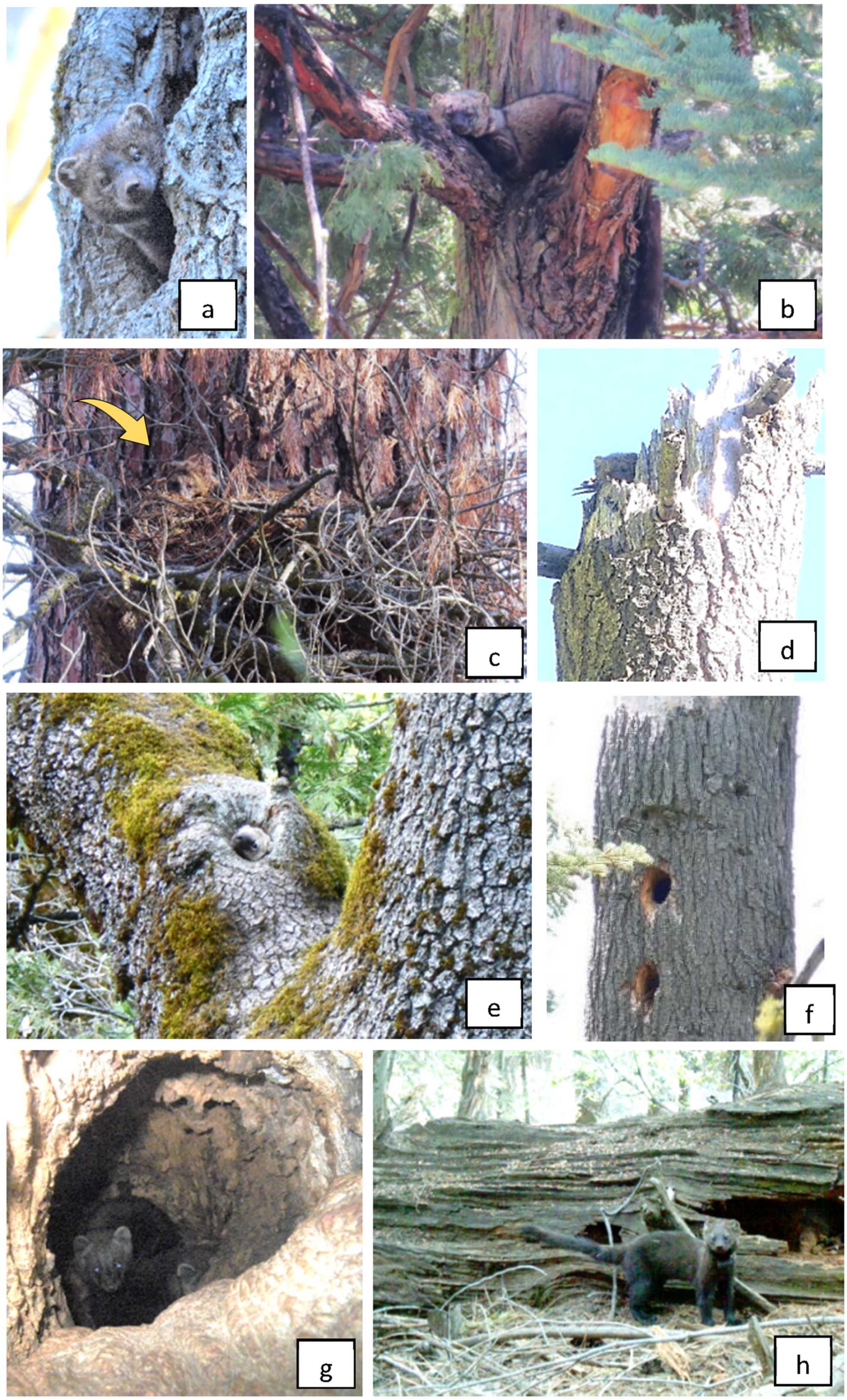


Fig. 2. Examples of microsites used by fishers in the southern Sierra Nevada. At rest structures, both sexes used (a) cavities in boles of trees and platforms associated with (b) large branches, (c) branch clusters, brooms, and nests (fisher at end of arrow), and (d) broken tops (fisher top left). At den structures, females used tree cavities accessed through (e) limb scars (fisher in cavity entrance) and (f) pileated woodpecker (*Dryocopus pileatus*) holes. Kits were reared in (g) cavities in the boles of trees. Near the end of the den season and in summer, females also used (h) cavities in logs to house kits. Photo credits: (a) L. Moon, (b through h) R. Green. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

next most common structure type was live conifer, while for maternal dens it was conifer snag (Fig. 4). Females used 6 tree species as den structures (Table 4); use by species did not differ for natal and maternal dens ($X_4^2 = 2.92$, $P = 0.57$; excluding canyon live oak due to low sample size). Females used California black oak most often for natal and maternal dens, followed by white fir then incense cedar (Table 4).

Natal and maternal den structures were similar in diameter (Table 3). Hardwoods used as reproductive dens were usually live but declining trees (class 2; natal 90.5%, maternal 92.6%). Conifers used as dens were also most frequently in live but declining trees (natal 67.5%,

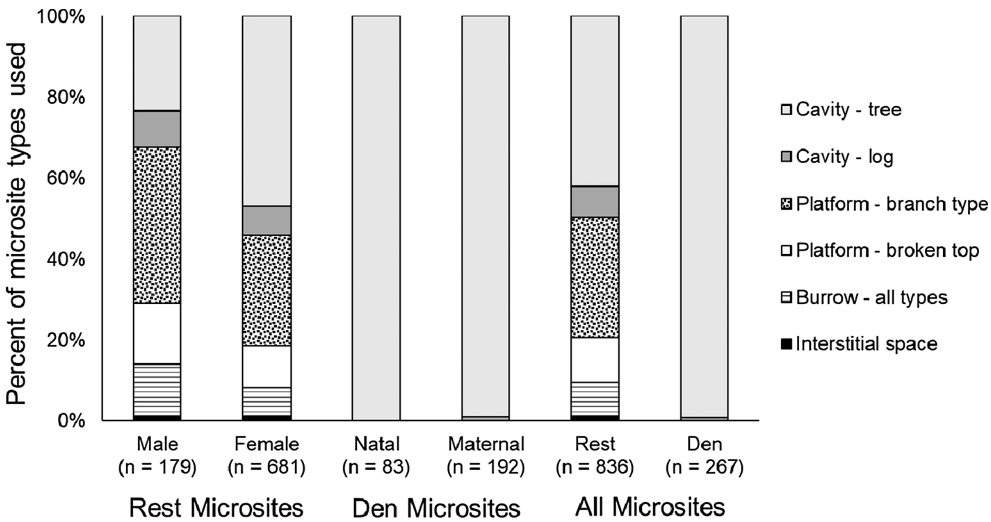


Fig. 3. Proportion of microsites used by fishers in the southern Sierra Nevada. Microsites were classified into 6 categories and separated here into microsites used for resting (males, females), denning (natal, maternal), and a comparison of rest combined to den combined. Branch type platforms include 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 but can occur in live trees. 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.

maternal 40.2%), though snags with varying levels of decay levels comprised over half of all maternal dens in conifers. Natal and maternal dens occurred on similarly steep slopes ($t_{270} = 1.04$, $P = 0.30$), and over comparable elevations (natal mean 1520 ± 230 SD, range 1020–2059 m versus maternal mean 1480 ± 224 SD, range 1013–2049 m; $t_{273} = -1.34$, $P = 0.18$; Table 3).

3.2.3. *Comparison – fine-scale habitat used by resting fishers (both sexes) and denning females*

Combined, males and females rested most often in tree cavity microsites (42.1%), then branch platforms (29.7%), and broken top platforms (11.1%). Reproductive females denned exclusively in cavity microsites (tree cavity 99.3%; log cavity 0.7%; Fig. 3, Table 2).

The proportion of structure types used by denning females ($n = 267$) differed from those used by resting fishers ($n = 910$; $X^2_5 = 90.24$, $P < 0.01$; Fig. 4, Table 2). Live conifers, live hardwoods, and conifer snags comprised the majority of both rest and den structures. However, live conifers were the most commonly used rest structures and live hardwoods made up nearly half of all den structures (Fig. 4). Resting fishers used a greater variety of tree species than did denning females, but California black oak and white fir were used more than any other species for both activities (Table 4). Proportional use differed for resting and denning ($X^2_5 = 68.39$, $P < 0.01$; for species used on > 5 occasions). California black oaks were used nearly twice as often for denning as for resting. In contrast, ponderosa pine was used more often for resting than for denning. White fir and incense cedar were used at similar frequencies for both activities (Table 4). Mean diameter was 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 C). Of note, live conifers used for denning were larger in diameter than those used for resting ($t_{292} = 4.21$, $P < 0.003$; Table 3).

Hardwoods used by fishers were generally live but declining (decay class 2), but showed greater variability for resting (69.7% class 2, 16.9% class 1) than denning (91.9% class 2). In contrast, conifers used for resting were most frequently in decay classes 1 (36.0%) or 2 (24.0%), while denning fishers used decay class 2 most often (48.3%). Although both rest and den structures commonly occurred in steep terrain, dens occurred on steeper slopes ($t_{876} = 4.50$, $P < 0.003$; Table 3). Within our study area, dens occurred at lower elevations than rest structures (denning mean 1494 ± 227 SD, range 1013–2059 m, resting 1541 ± 250 SD, range 965–2555 m; $t_{1162} = -2.65$, $P = 0.008$; Table 3).

Table 3
Characteristics of fisher microsites and structures used for resting and denning in the southern Sierra Nevada (2007–2015). Fisher use was grouped into 3 comparisons: male and female rest, natal and maternal den, and rest combined and den combined. Tree measurements were subdivided into hardwood or conifer species, and live or dead structures, due to potential differences between these categories. Microsites or structures used on > 1 occasion were counted once per category. We used a Bonferroni-adjusted *P* value of 0.005 for significance, reflecting an alpha of 0.05 and 11 tests; bold letters denote statistical differences.

Habitat characteristics	Rest microsites and structures Mean ± SD (*n*)		Den microsites and structures Mean ± SD (*n*)		All microsites and structures Mean ± SD (*n*)	
	Male	Female	Natal	Maternal	Rest Combined	Dens Combined
Microsite height (m)						
All (tree, ground)	8.8 ± 7.6 (*104*)	8.9 ± 8.0 (*354*)	11.2 ± 9.3 (*67*)	9.1 ± 6.9 (*171*)	8.8 ± 7.8 (*443*)	9.7 ± 7.8 (*231*)
Hardwood – Live	7.3 ± 4.4 (*23*)	7.1 ± 5.7 (*111*)	6.8 ± 2.4 (*33*)	6.7 ± 3.5 (*94*)	7.1 ± 5.5 (*131*)	6.7 ± 3.3 (*125*)
Hardwood – Snag	6.3 ± 4.2 (*4*)	5.4 ± 1.8 (*12*)	4.5 ± 2.3 (*3*)	7.0 ± 3.2 (*6*)	5.6 ± 2.5 (*15*)	6.1 ± 3.1 (*9*)
Conifers – Live	16.2 ± 6.2 (*33*)	17.1 ± 7.2 (*90*)	18.5 ± 12.2 (*22*)	16.7 ± 10.2 (*29*)	16.7 ± 6.9 (*116*)	17.9 ± 11.1 (*48*)
Conifer – Snag	10.4 ± 4.9 (*18*)	10.3 ± 5.7 (*72*)	12.0 ± 7.8 (*9*)	10.0 ± 6.4 (*40*)	10.4 ± 5.5 (*88*)	10.4 ± 6.7 (*47*)
Structure dbh (cm)						
Hardwood – Live	83.0 ± 19.5 (*30*)	75.8 ± 20.6 (*153*)	79.1 ± 20.6 (*38*)	75.0 ± 17.7 (*101*)	76.6 ± 20.5 (*180*)	76.3 ± 18.6 (*137*)
Hardwood – Snag/Log	74.3 ± 16.8 (*4*)	73.7 ± 22.7 (*22*)	62.6 ± 6.0 (*4*)	72.5 ± 14.0 (*8*)	74.4 ± 21.8 (*25*)	69.2 ± 12.6 (*12*)
Conifer – Live	92.6 ± 30.3 (*64*)	95.8 ± 34.5 (*181*)	115.6 ± 27.7 (*28*)	111.5 ± 20.4 (*36*)	**94.9 ± 33.6 (*234*)**	**113.4 ± 24.3 (*60*)**
Conifer – Snag/Log	**127.2 ± 47.4 (*37*)**	**100.3 ± 28.5 (*154*)**	108.3 ± 32.2 (*13*)	103.4 ± 28.6 (*47*)	105.5 ± 34.8 (*185*)	104.8 ± 29.6 (*58*)
Topography at structure						
Elevation (m a.s.l.)	**1602 ± 302 (*191*)**	**1524 ± 232 (*731*)**	1520 ± 230 (*83*)	1480 ± 224 (*192*)	1541 ± 250 (*898*)	1494 ± 227 (*267*)
Slope (%)	32.6 ± 17.1 (*143*)	32.0 ± 17.7 (*495*)	35.1 ± 16.0 (*82*)	37.3 ± 16.0 (*190*)	**32.0 ± 17.6 (*616*)**	**36.6 ± 15.9 (*264*)**

Table 4
Fisher use of structures (live tree, snag, log) by tree species in the southern Sierra Nevada for resting and denning. The table displays comparisons of structures (a) used by male and female fishers for resting, (b) used by reproductive females for natal and maternal dens, and (c) used for resting (male and female combined) and those used for denning (natal and maternal combined). Structures used on > 1 occasion by a fisher were counted only once per category.

Tree species	Rest structures		Den structures		All structures	
	Male (n = 171)	Female (n = 674)	Natal (n = 83)	Maternal (n = 192)	Rest combined (n = 822)	Den combined (n = 267)
California black oak	24.0%	31.0%	49.4%	56.8%	29.9%	55.4%
Canyon live oak	1.2%	2.1%	1.2%	0.0%	1.9%	0.4%
Incense cedar	8.8%	13.5%	16.9%	10.9%	12.7%	11.6%
Ponderosa pine	25.1%	17.5%	4.8%	6.3%	18.6%	6.0%
Sugar pine	9.4%	5.3%	3.6%	2.1%	6.2%	2.6%
White fir	28.1%	29.2%	24.1%	24.0%	28.8%	24.0%
Other species	3.5%	1.3%	0.0%	0.0%	1.8%	0.0%

3.3. *Role of tree species in providing suitable microsites and structures for fishers*

Combining structures used for resting and denning, we found patterns of microsite use varied by tree species in ways that reflected patterns of growth and decay (Fig. 5). Generalizing microsite types from all structures (rest and den) into cavity or platform categories, we found that microsite type varied across the most commonly used tree species (n = 1029; $X_5^2 = 293.4$, $P < 0.01$). Oak species were unique in that they disproportionately provided tree cavity microsites (California black oak 91.7%, Canyon live oak 66.7%; Fig. 5). White fir and incense cedar were similar in providing a high proportion of tree cavities (52.3% and 50.4% respectively) and branch type platforms (22.5% and 19.1% respectively); they differed in that white fir also provided more broken top platforms (20.9%) while incense cedar yielded more log cavities (23.7%; Fig. 5). Pine species differed from other tree species in yielding fewer tree cavity microsites (ponderosa pine 18.2%, sugar pine 29.1%), but they were a common source of branch type platforms (ponderosa pine 68.4%, sugar pine 56.4%; Fig. 5). As might be expected, den structures of different tree species varied by elevation (excluding species with $n < 10$, $F^3_{263} = 23.4$, $P < 0.01$; Fig. 6). Sugar pines (1708 m ± 156 SD) and white firs (1649 m ± 190 SD) were used at higher elevations of our study area, followed by incense cedar (1559 m ± 200 SD) and ponderosa pine (1500 m ± 248 SD) at middle elevations. California black oak (1406 m ± 199 SD) and Canyon live oak (1138 m ± 0 SD) more commonly used at lower elevations.

4. Discussion

Our investigation of fine-scale habitat use by fishers in the southern Sierra Nevada corroborates patterns found in other parts of the range and provides new data to support forest management and fisher conservation in this region. As noted elsewhere, our findings emphasize the contributions of large diameter trees and processes of decay in creating daily refuges and reproductive dens for this rare species (Zielinski et al., 2004a; Weir et al., 2012; Gess et al., 2013). The affiliation between denning female fishers and features of older trees has been documented previously (e.g., in British Columbia; Weir et al., 2012). Our study confirms that mature forest elements are still critical for reproduction in the more xeric conditions at the southernmost extent of this species' distribution, but that tree characteristics (species, size) differ from other regions.

Prior to the initiation of this study in 2007, as few as 6 fisher reproductive dens had been documented in the Sierra Nevada, thus data of local relevance were extremely limited (Grinnell et al. 1937; Truex et al. 1998). Although we expected (and found) that hardwoods provided over half of all den structures (51%), this percentage was lower than other geographic areas. For comparison, Matthews et al. (in review), documented 73% of den structures (n = 406) as hardwoods in northern California with tan oak (*Notholithocarpus densiflorus*) being used most often. The proportion of hardwoods used as reproductive dens was even higher in Maine at 94% (n = 33; Paragi et al.,1996) and in British Columbia at 100% ((n = 31; Weir et al., 2012); in both studies, aspen (*Populus tremuloides*) was the most commonly used species. These comparisons emphasize that while hardwoods are important in providing den structures for fishers, conifers play a bigger part in the southern Sierra Nevada compared to other parts of the range. We also found substantial differences in den tree diameter with our local data compared to other regions. The average diameters of live hardwoods (76 cm) and live conifers (113 cm) used as dens in our study were quite a bit larger than those found in British Columbia and Maine (range 45–60 cm). These findings emphasize the value of local or regional data for use in forest planning as they reflect available tree species that were grown under comparable environmental conditions.

There are several unique aspects of our dataset and analysis that are worth emphasizing. First, the long-term nature of our study allowed us to monitor over 100 individual fishers and include year-round data in the same area for an extended period (8 years) over a variety of conditions (e.g., weather, human disturbance, variation in prey, predators, and conspecifics). As a result, these data may better represent the variety of habitat elements needed to sustain a local fisher population over time than a study of shorter duration or with fewer individuals. Second, few studies have compared habitat elements used by denning females to those used by resting fishers (males, females) within the same landscape. This approach emphasizes the multiple fine-scale habitat needs of a local population while also highlighting the unique needs of females during reproduction. Third, we developed general predictions about the microsite needs of males and females based on factors related to sexual dimorphism and coarse estimates for the physical and thermal properties of microsite types. We found patterns that mostly fit our expectations that resting females would use microsites with greater protection more often than males, and that denning females would only use microsites with considerable physical and thermal protection.

4.1. *Variation in use of microsites and structures within a fisher population*

While we wanted to provide descriptive information on the microsites and structures used by reproductive females in the southern Sierra Nevada, we also wanted to explore the degree of specialization in the fine-scale habitat used within a local fisher population for resting and denning activities. Understanding the diversity of structures needed by fishers on a landscape can help ensure that multiple population needs are met. Revisiting the conceptual models associated with specialization in structure use (Appendix A), data from the Sierra Nevada appear to fit best with panel D, which indicates some overlap in structure use across groups (resting males, resting females, maternal dens, natal dens), but also some specialization of each group. Specifically, our data suggest that the types of structures used by resting males and females share many similar characteristics, indicate some specialization, and generally exhibit greater variation than den structures. In contrast, structures used as natal and maternal dens each represent smaller

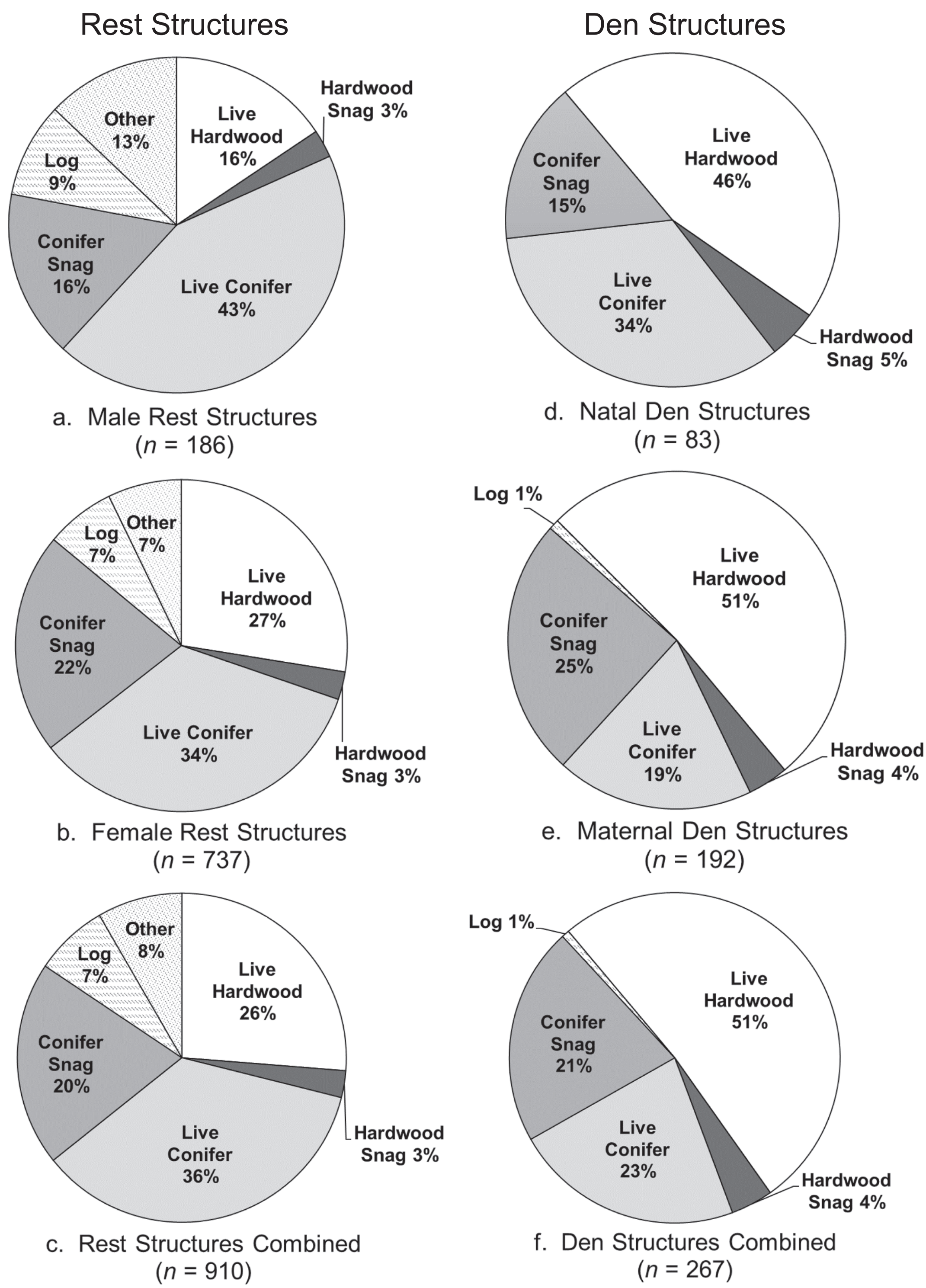


Fig. 4. Types of structures used by fishers for resting (males, females, and sexes combined, (a–c) relative to those selected by females denning (natal, maternal and combined (d–f) in the southern Sierra Nevada. Log includes both hardwood and conifer species, and Other includes ground-level structures such as rock piles, ground burrows, or slash piles. Structures used on > 1 occasion were counted once per category.

subsets of the available pool of structures, exhibiting extensive overlap with each other and with structures used by resting females (cavity rest structures). Our findings indicate that rest structures may be easier to maintain on a landscape because the pool of suitable options is larger than for den structures. However, our results also suggest that maintaining a diverse pool of large trees with hollows may serve multiple purposes (potential natal dens, maternal dens, or cavity rest structures for females or males).

4.2. Microsites and structures used by male and female fishers for resting

Male and female fishers exhibited similarities in the types of microsites used for resting, but also demonstrated specialization that could be tied to sexual dimorphism. Females frequently chose microsites that appeared to offer more physical protection (e.g., cavities) than those used most often by males (e.g., platforms), a pattern also found by Zielinski et al. (2004a). Risk of predation by multiple species could

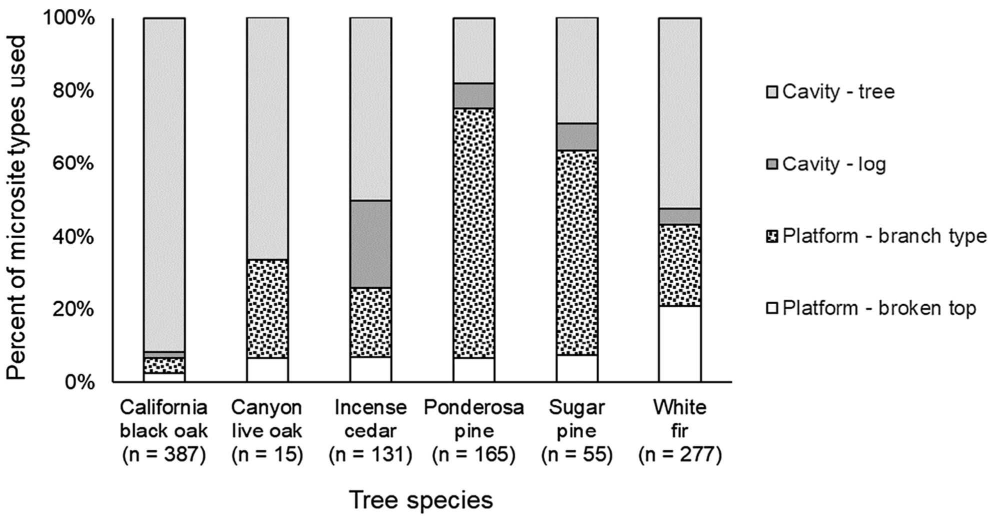


Fig. 5. Distribution of microsite types within tree species used by fishers for resting or denning (combined) in the southern Sierra Nevada. Microsites used on > 1 occasion by a fisher were counted only once per category and only tree species associated with ≥ 5 microsites were included. In California black oak, tree cavities were used disproportionately by fishers. Branch type platforms were frequently used in ponderosa pine, and white fir provided a nearly equal mix of cavity and platform microsites.

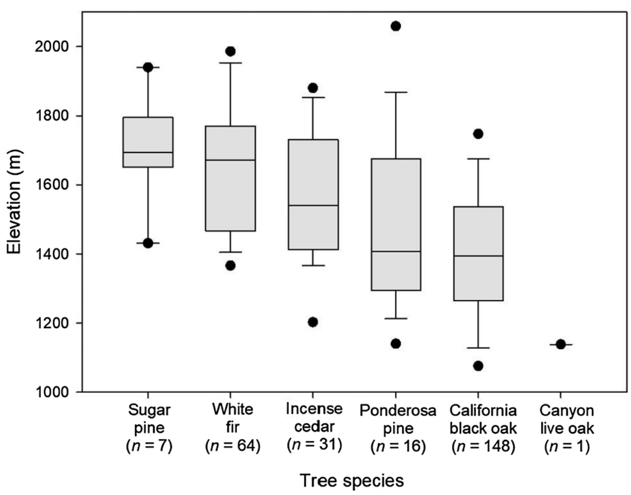


Fig. 6. Box plots displaying the elevation range of structures used as reproductive dens (natal and maternal combined) by female fisher in the southern Sierra Nevada separated by tree species. Although there was overlap in the elevation range of the tree species used most often by fishers for denning, white fir was used more frequently at higher elevations while California black oak was more commonly used at lower elevations. Boxes represent the 25th and 75th percentiles, horizontal lines represent median values, whisker bars denote the 10th and 90th percentiles, and outliers within the 5th to 95th percentile range are shown with black dots. Structures used on > 1 occasion by a fisher were counted only once.

explain the tendency for smaller-bodied females to use more tree cavities than the larger-bodied males. Branch platforms and broken tops may have unique benefits (e.g., good vantage points to observe prey or predators), but are unlikely to provide the same level of physical security as the enclosed space in tree cavities. Males also used ground burrows more often than females; although these microsites offered some security, there may be greater risks associated with ground level entrances compared to tree cavities. In regards to thermal protection, enclosed microsites such as tree cavities, log cavities, burrows, and subnivean spaces are all known to buffer cold ambient temperatures (Weir et al., 2004; Joyce et al., 2017; Green, 2017). Platforms allow for sun exposure on cool days or access to a breeze on hot days, but cavities offer thermal stability, making them an energy efficient choice for smaller-bodied females. Last, male fishers often appeared to choose microsites that fit a larger body, or conversely, they may have been excluded from microsites that were accessible to females. As corroboration, several studies have documented that the broader head size of adult male fishers would prevent them from entering the small entrances at natal den microsites, thus the same may be true at rest microsites (Green, 2017; Matthews et al. (in review)).

Structures used for resting by males and females were similar in many ways, but with some specialization of each group. Females used hardwood trees most often for resting, but males also used them regularly and both sexes relied on hardwoods (largely California black oaks) as a source of cavity microsites. Conifers (particularly white fir and ponderosa pine) were commonly used by both sexes, with males especially reliant on live trees for branch platforms and females commonly using snags as a source of cavities. White fir provided a variety of microsite types in live trees and snags while ponderosa pine most often yielded branch platforms in live trees. Live conifers used by males and females were large (but variable) and did not differ by sex, but the diameter of conifer snags and logs used by males were larger than those used by females, suggesting that a minimum size is needed to develop broken top platforms or cavities suitable for males.

Standing trees comprised most rest structures in our study area, but ground level structures were used by both sexes, though less frequently than in other geographic areas perhaps due to less severe winters in the southernmost portion of the range (Joyce et al., 2017). Large logs (hardwood and conifer) with hollows provided a unique function in supporting the later stages of reproduction, in that we documented females with mobile kits using them as maternal rest structures in summer and fall. The horizontal position of the hollow in logs may better accommodate females with mobile young (or adult males) and provide an accessible refuge for kits that are not yet agile climbers. Less frequently, fishers used spaces under suspended logs, natural log piles, and human-created slash piles that may serve a similar function but have less physical or thermal protection. Slash piles used in our study area were quite large; as examples, 2 piles composed of small diameter trees were 5 m tall and were 13 × 29 m and 33 × 51 m in area, respectively.

4.3. Microsites and structures used by reproductive female fishers as natal and maternal dens

Paralleling previous studies, all natal and maternal den microsites were in tree cavities, with the exception of 2 late season maternal dens in log cavities. As found by Powell et al. (1997) in New England, cavity entrances of dens initiated early in the season tended to be higher than those initiated later, suggesting the needs of reproductive females may shift as the den season progresses. Tree cavities with higher entrances may provide greater physical protection by restricting access for terrestrial predators. Higher cavities may have greater solar exposure than lower cavities, potentially offering increased warmth early in the den season when kits are small and temperatures can be cold. Many birds experience increased fledgling survival with higher nest placement, including species using tree cavities (Li and Martin, 1991; Fisher and Wiebe, 2006; Cockle et al., 2015). Lower cavities may appeal to females late in the den season as kits increase in size and become unwieldy to carry. When kits begin learning to climb, lower entrances may also minimize accidents. Similar patterns of behavior were noted for American martens in Maine; female martens with kits shifted from denning in tree cavities to ground level logs during the period when kits were still learning to climb (Wynne and Sherburne, 1984).

Structures used as natal dens were very similar to those used as maternal dens, perhaps because trees with cavities large enough for female fishers are likely to be in the species most prone to cavity development, be restricted to a minimum diameter, and exhibit a moderate level of decay. Large diameter California black oaks comprised nearly all hardwood natal and maternal den structures in our study area, indicating that they provide features of value to females throughout the den season. Conifers (particularly white fir and incense cedar) comprised roughly half of all remaining den structures, with live conifers used more often as natal dens and conifer snags used more frequently for maternal dens. The tendency for females to use live trees (hardwoods and conifers) as dens (especially at natal dens) could be because they provide greater physical security and thermal protection than snags. For example, 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. However, snags may have increasing benefits to females later in the den season when the need to protect kits from cold temperatures decreases and qualities associated with more decay (e.g., lower cavity entrances, larger interior chambers) increase in value in parallel with the increasing size and mobility of kits.

4.4. Microsites and structures used by fishers for resting compared to denning

As documented in other areas (e.g., Paragi et al., 1996; Powell et al., 2003; Weir et al., 2012), cavities in tree boles are critical for fisher reproduction in the southern Sierra Nevada. In contrast, resting fishers used an assortment of microsite types with (apparently) varying levels of physical security, thermal benefits, and accessibility to fishers of different sizes. Compared with other microsite types used for resting, tree cavities appear to offer the most physical and thermal protection for female fishers with kits. This observation is supported by data collected at fisher den cavity microsites within our study area (Green, 2017) and in northern California (Matthews et al., in review), as well as by researchers studying the insulative properties of tree cavities in general (Coombs et al., 2010; Maziarz and Wesolowski, 2013). We have some evidence that females use prior experience in selecting den microsites, as we occasionally documented females resting in tree cavities that were later used for denning. Prior experience would allow females to assess the cavity interior and consider whether the entrance would exclude males, a potentially desired characteristic at natal dens due to the timing of mating soon after parturition. Anecdotally, we documented male fishers resting on platforms in natal den trees during the mating period while a female was in a cavity of the tree. These cases indicate that structures may contain multiple microsites and serve multiple functions (i.e., denning and resting).

Notably, we had a greater sample size of rest structures for females than males in our study, and a greater number of rest structure for females in the spring denning period compared to other seasons. Because we grouped all of these rest structures together for this comparison with den structures, our rest structure data are biased towards females and the spring season. However, from a conservation perspective at a population level this bias towards females in general and a time period that supports reproduction may be justified. In other words, erring on the side of maintaining structures suitable for females to use just prior to denning, or during the mating period for females that are not denning, has benefits from a population perspective. Additionally, female home ranges are much smaller than males, so maintaining more structures that are suitable for females on the landscape may benefit the population (Zielinski et al., 2004b). The structures used for resting and denning had some similarities, but den structures always had cavities in the bole of the tree thus were consistently associated with large diameters while rest structures could have either cavity or platform microsites so were more variable in size. Of the hardwoods, large decadent California black oaks provided the most cavities for denning, but they also supplied tree and log cavity microsites for resting males and females throughout the year. Of the conifers, white firs and incense cedars were key sources of cavities (especially at higher elevations) as well as platforms, while pine species provided mostly platform microsites so were used most often for resting. Rest and den structures occurred on steep slopes, but this was more pronounced at dens. Dens on steep slopes may offer favorable microclimates due to increased solar radiation, provide a vantage point for females to assess threats prior to leaving the den, or reflect historic management as trees on steep slopes would have been less accessible to logging equipment in the past.

4.5. Tree ecology, forest management, and sources of fine-scale habitat for fishers

Tree species differ in their ecology, distribution, patterns of growth, and vulnerability to decay (Oliver and Larson, 1996). Correspondingly, the tree species used by fishers in our study area varied in the types of microsites they provided for resting or denning. Of the hardwoods, California black oaks were conspicuous as a source of tree cavities suitable for fishers. In comparison, we rarely found fishers in cavities of canyon live oak, perhaps because this species is less susceptible to heart rot or trees in our study area were too small. Our findings reinforced the importance of hardwoods for denning and resting (especially in lower elevations), but also underscore that not all hardwood species are equivalent in providing cavity microsites in this region. 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., 2009). We are unaware of data on how long it takes for hollows to form in California black oaks, but the study by Ranius et al. (2009) emphasizes the exceptional amount of time that may be required for structures of sufficiently large diameter to grow and form cavities suitable for fishers. Fostering growth of California black oaks that can develop suitable hollows may help to eventually replace the declining trees currently used by fishers in this region.

In contrast, multiple conifer species were used regularly in our study area. White fir was the conifer used most often for resting and denning, but large diameter ponderosa and sugar pines were selectively removed from Sierra Nevada forests in the past. Pines may have played a more important role as sources of cavities when large (old) trees were more common in these forests (McKelvey and Johnston, 1992). Alternatively, these patterns may reflect differences in capacity to develop certain microsites (i.e., cavities versus platforms) or persist over time. In this study, white firs yielded more cavities used by fishers than any other local conifers, perhaps due to their susceptibility to heart rot (Laacke, 1990). However, incense cedars which develop suitable cavities appear to remain available for many years due to their high resistance to decay (McDonald, 1973). Incense cedars also yielded a disproportionate number of log cavities; the wood of incense cedar is hard and resistant to decay, thus standing trees which develop hollows often retain their shape when they fall and last longer as logs than other conifers (McDonald, 1973). Conifer distribution is associated with elevation in the Sierra Nevada. White firs were widespread in higher elevations used by fishers in our study, providing tree cavity and platform microsites in this conifer dominated elevation band. Sugar pines were also used at higher elevations, supplying branch platforms and a moderate number of cavities. Incense cedars were used at middle elevations and may be an important source of cavities where California black oaks are uncommon. Ponderosa pines were most common at mid- to low elevations and were largely associated with branch platforms.

Maintaining the ecological pathways that facilitate the creation of cavity microsites is important for fishers and other wildlife that utilize cavities (Cockle et al., 2012; Bunnell, 2013). The heartwood decay that forms cavities in trees and logs is initiated in living trees (McDonald, 1990; Hennon, 1995). So, for the large chambers in tree boles used by fishers to form, decay must occur before a tree dies; the hollows in logs are also generated while trees are still standing, and for the hollow to remain usable the chamber must remain intact after a tree falls (Bull et al., 1996; Ranius et al., 2009). Although the process varies by species, fungi that lead to heartwood decay may gain entry and/or be facilitated by death of limbs or other damage (e.g., fire scar, physical injury). Related factors help create fisher-sized access points to hollows (e.g., excavations by pileated woodpeckers (*Dryocopus pileatus)*, large limbs breaking off, and broken trunks; McDonald, 1990; Oliver and Larson, 1996; Bonar, 2000; Remm and Lõhmus, 2011). In general, older trees are more susceptible to heartwood decay than younger trees, and hardwoods are more prone to heart rot than conifers; characteristics of individual tree species and local climatic conditions may also influence the rate or prevalence of decay (Oliver and Larson, 1996; Remm and Lõhmus, 2011; Bunnell, 2013). In the Sierra Nevada, heart rot affects conifer species but is perhaps more commonly observed in hardwoods such as California black oak (Laacke and Fisk, 1983; McDonald, 1990). In areas where retaining trees that contain (or may develop) cavities suitable for fishers is a goal, a basic understanding of these processes combined with an assessment of individual trees for signs of heart rot or potential cavity entrances could support conservation of appropriate habitat elements (Laacke, 1990; Bunnell et al., 2002).

Identifying and retaining trees with suitable platform microsites can also contribute to providing habitat elements needed by fishers for resting in managed landscapes (Aubry et al., 2018). We could not always identify with certainty what factors formed individual branch clusters, but known causes of brooms include disease (fungi, rusts), parasites (dwarf mistletoe), and other organisms (Tinnin et al., 1982; Laacke and Fisk, 1983; McDonald, 1990; Tinnin and Forbes, 1999). Individual branches used by fishers tended to be wide (≥ 12 cm), thus associated with large trees. "Stick nests" were clusters of pine needles, deciduous leaves, or sticks that may have been assembled by other animals (e.g., squirrel, raptor) or collections of litter caught in a branch cluster or adjacent to the trunk; similar features were used by fishers in Oregon (Aubry et al., 2018). Broken tops used by fishers in live trees and snags contained flat areas where fishers could hide from view; only large old trees appeared to yield broken tops with sufficient room for fisher-sized platforms. Processes of decay combined with wind events and tree height may all contribute to the formation of broken top platforms suitable for fishers (Hennon, 1995).

5. Conclusions

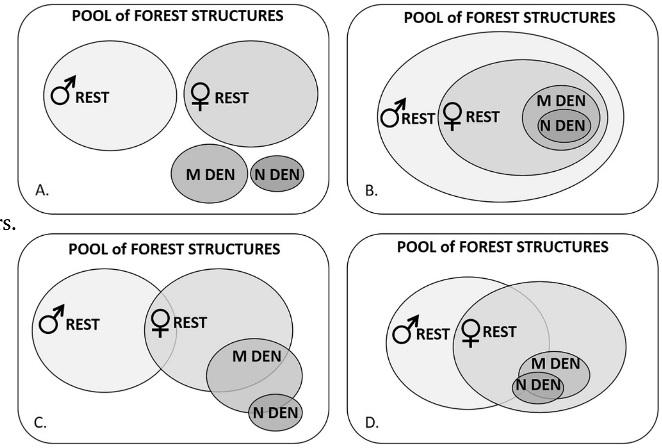
Roughly a century of fire suppression, timber harvest, and development across forests in the western United States has led to changes in species composition, size class distribution, and the availability of large decadent trees (Parsons and DeBenedetti, 1979; Ansley and Battles, 1998; Scholl and Taylor, 2010). In recent years, drought conditions followed by 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 consider some steps that may help support reproduction and resting activities of fishers. First, retention of large diameter live trees and snags with some level of decay can help maintain availability of both rest and den structures. Many of the microsites and structures used by fishers for resting, and virtually all those used by females for denning, require extensive time and a unique series of ecological processes to develop and once lost, cannot be easily or quickly replaced (Manning et al., 2013). Prioritizing for retention trees with signs of suitable cavity microsites (e.g., large broken limbs, pileated woodpecker holes) or other potential microsites may benefit fishers. Second, long-term plans to replace existing structures may be needed to ensure that suitable forest elements are available for fishers in the future. Existing trees will eventually be lost to decay or other factors (e.g., beetle kill), and recruitment may play a key role in places where large diameter trees are limited. Third, some tree species may warrant greater prioritization in plans to protect or recruit fisher den and rest structures. California black oak, white fir, and incense cedar were used most often for denning and their distribution varies by elevation; maintaining a well-distributed supply of large diameter trees of these species may help ensure availability of cavity microsites. As California black oak and incense cedar also have greater drought tolerance than other available species, focusing on these species may prove beneficial under predicted warmer and drier climatic conditions (McDonald, 1990; Powers and Oliver, 1990; Mann and Gleick, 2015). Finally, plans to maintain forest elements for fishers should include elevation due to its relationship with tree species distribution, precipitation, and the current extent of tree mortality.

Acknowledgements

We would like to thank the many field assistants that helped in fisher monitoring and measurement of vegetation at reproductive dens and rest structures, including J. Banaszak, W. Binder, T. Brickley, S. Brink, A. Calderon, A. Chong, A. Eichle, J. Garner, N. Hebert, C. Indelicato, J.P. Jones, L. Kerschner, J. Kordosky, C. Larsen, J. Latter, M. Linnell, L. McCardle, G. Merrill, L. Moon, J. Nawrocki, B. Nichols, A. Reyes, S. Rossler, E. Soto, J. Schneiderman, T. Smith, Z. Stoll, R. Tebo, L. Van Vranken, M. Webber, and S. Wong. We are especially grateful to Z. Miller and W. Watts for assuming leadership roles in collecting vegetation data. We appreciate the statistical advice of J. Baldwin (USDA Forest Service, Pacific Southwest Research Station). We acknowledge L. Moon for the photo used in Fig. 2a. We thank S. Byrd and Southern California Edison for access to their land in conducting this research. Financial and logistical support was provided largely from the United States Forest Service Region 5. R.E.G. acknowledges financial support from the American Society of Mammalogists (Grants-in-Aid of Research), the University of California, Davis (Jastro-Shields award), and a Walter and Elizabeth Howard Wildlife Management Award through the Department of Wildlife, Fish, and Conservation at University of California, Davis.

Appendix A

Conceptual models showing possible relationships between four categories of forest structures used by fishers: rest structures used by males, rest structures used by females, and natal and maternal dens used by reproductive females. Model A shows a high degree of specialization for each group. Model B shows considerable overlap of groups, but with specialization of den structures. Models C and D represent other combinations of overlap and specialization in structure use relative to a larger pool of available structures at a local level. These models can help illuminate similarities and differences in fine-scale habitat needs of fishers.



Appendix B

Summary of the types of microsites used by male and female fishers for resting throughout the year 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 % (*n*)		
	Male (*n* = 199)	Female (*n* = 763)	Combined (*n* = 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 (“stick nest”)	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 C

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 ± SD (range)	M (*n*)	F (*n*)	Mean ± SD (range)	ND (*n*)	MD (*n*)
Live tree						
Hardwood						
Big leaf maple	43.0 ± 8.5 (37.0–49.0)	0	2			
California black oak	78.7 ± 19.5 (35.2–163.0)	28	140	76.0 ± 18.5 (40.1–134.5)	37	101
Canyon live oak	58.2 ± 24.8 (25.0–97.0)	1	6	98.0 (0)	1	0
White alder	59.1 ± 22.3 (38.5–87.5)	1	3			
Conifer						
Incense cedar	116.3 ± 39.8 (42.0–204)	8	29	124.3 ± 21.7 (88.0–153.2)	10	9
Jeffrey pine	88.2 ± 23.9 (66.0–113.5)	2	1			
Ponderosa pine	88.2 ± 31.0 (36.5–184.5)	27	63	117.4 ± 23.5 (74.9–139.8)	3	4
Sugar pine	104.0 ± 34.4 (52.0–155.1)	7	15	123.0 ± 13.8 (107.3–133.4)	1	2
White fir	90.7 ± 28.9 (18.0–184.5)	17	69	105.7 ± 23.5 (67.5–160.0)	14	20
Snags and Logs						
Hardwood						

California black oak	74.1 ± 21.9 (43.5 – 136.0)	3	21	69.2 ± 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 ± 33.6 (29.5–199.0)	5	34	102.8 ± 23.0 (73.1–148.5)	4	12
Jeffrey pine	138.8 (0)	0	1			
Ponderosa pine	99.4 ± 26.4 (47.5–145.0)	5	20	96.5 ± 29.0 (46.6–129.5)	1	8
Red fir	137.4 (0)	0	1			
Sugar pine	130.5 ± 27.8 (89.0–180.0)	5	8	138.4 ± 22.6 (72.2–169.7)	2	2
White fir	105.0 ± 30.2 (55.0–171.7)	22	83	103.3 ± 28.5 (53.5–150.4)	6	26

References

Ansley, J.S., Battles, J.J., 1998. Forest composition, structure, and change in an old-growth mixed conifer forest in the northern Sierra Nevada. J. Torrey Bot. Soc. 125, 297–308.

Asner, G.P., Brodrick, P.G., Anderson, C.B., Vaughn, N., Knapp, D.E., Martin, R.E., 2016. Progressive forest canopy water loss during the 2012–2015 California drought. Proc. Natl. Acad. Sci. 113, E249. https://doi.org/10.1073/pnas.1523397113.

Aubry, K.B., Raley, C.M., 2006. Ecological characteristics of fishers (Martes pennanti) in the southern Oregon Cascade Range. U.S.D.A. Forest Service, Pacific Northwest Research Station, Olympia Forestry Sciences Laboratory. Update. Olympia, Washington.

Aubry, K.B., Raley, C.M., Buskirk, S.W., Zielinski, W.J., Schwartz, M.K., Golightly, R.T., Purcell, K.L., Weir, R.D., Yaeger, J.S., 2013. Meta-analyses of habitat selection by fishers at resting sites in the Pacific Coastal Region. J. Wildl. Manage. 77, 965–974.

Aubry, K.B., Raley, C.M., Cunningham, P.G., 2018. Selection of rest structures and microsites by fishers in Oregon. J. Wildl. Manage. 82, 1273–1284.

Bonar, R.L., 2000. Availability of pileated woodpecker cavities and use by other species. 2000. J. Wildl. Manage. 64, 52–59.

Brown, J.H., Lasiewski, R.C., 1972. Metabolism of weasels: the cost of being long and thin. Ecology 53, 939–943.

Bull, E.L., Akenson, J.J., Betts, B.J., Torgersen, T.R., 1996. The interdependence of wildlife and old-growth forests. Pp. 71–76 in Proceedings of the workshop on wildlife tree/stand-level biodiversity (P. Bradford, T. Manning, B. I'Anson, editors). British Colulmbia Ministry of Environment, Lands, and Parks and Ministry of Forests, Victoria, BC.

Bunnell, F.L., Wind, E., Wells, R., 2002. Dying and dead hardwoods: their implications to management. Pp. 695–716 in Proceedings of the symposium on the ecology and management of dead wood in western forest (W. F. Laudenslayer, P.J. Shea, B.E. Valentine, C.P. Weatherspoon, T.E. Lisle, technical coordinators). General Technical Report PSW-GTR-181. Pacific Southwest Research Station, Forest Service, U.S. Department of Agriculture, Albany, CA.

Bunnell, F.L., 2013. Sustaining cavity-using species: patterns of cavity use and implications to forest management. ISRN Forestry, article 457698. http://dx.doi.org/10.1155/2013/457698.

Clement, M.J., Castleberry, S.B., 2013. Summer tree roost selection by Rafinesque's big-eared bat. J. Wildl. Manage. 77, 414–422.

Cockle, K.L., Martin, K., Drever, M.C., 2010. Supply of tree-holes limits nest density of cavity-nesting birds in primary and logged subtropical Atlantic forest. Biol. Conserv. 143, 2851–2857.

Cockle, K., Martin, K., Wiebe, K., 2011a. Selection of nest trees by cavity-nesting birds in the Neotropical Atlantic Forest. Biotropica 43, 228–236.

Cockle, K.L., Martin, K., Wesołowski, T., 2011b. Woodpeckers, decay, and the future of cavity-nesting vertebrate communities worldwide. Front. Ecol. Environ. 9, 377–382.

Cockle, K.L., Martin, K., Robledo, G., 2012. Linking fungi, trees, and hole-using birds in a Neotropical tree-cavity network: pathways of cavity production and implications for conservation. For. Ecol. Manage. 264, 210–219.

Cockle, K.L., Bodrati, A., Lammertink, M., Martin, K., 2015. Cavity characteristics, but not habitat, influence nest survival of cavity-nesting birds along a gradient of human impact in the subtropical Atlantic Forest. Biol. Conserv. 184, 193–200.

Coombs, A.B., Bowman, J., Garroway, C.J., 2010. Thermal properties of tree cavities during winter in a northern hardwood forest. J. Wildl. Manage. 74, 1875–1881.

Cornelius, C., Cockle, K., Politi, N., Berkunsky, I., Sandoval, L., Ojeda, V., Rivera, L., Hunter Jr., M., Martin, K., 2008. Cavity-nesting birds in neotropical forests: cavities as a potentially limiting resource. Ornitologia Neotropical 19, 253–268.

Davis, L. R., 2018. Fisher (Pekania pennanti) artificial reproductive den box study. Report prepared for Habitat Conservation Trust Foundation, Fish and Wildlife Compensation Program, and Forest Enhancement Society of British Columbia. 29 pp.

de la Parra-Martínez, S.M., Renton, K., Salinas-Melgoza, A., Muñoz-Lacy, L.G., 2015. Tree-cavity availability and selection by a large-bodied secondary cavity-nester: the military macaw. J. Ornithol. 156, 489–498.

Erb, J., P. Coy, B. Sampson, 2015. Reproductive ecology of fishers and American martens in Minnesota. Pp. 153–165 in Summaries of wildlife research findings 2015 (L. Cornicelli, M. Carstensen, G. D'Angelo, M. A. Larson, and J. S. Lawrence, Eds.). Minnesota Department of Natural Resources, St. Paul, Minnesota.

Fisher, R.J., Wiebe, K.L., 2006. Nest site attributes and temporal patterns of northern flicker nest loss: effects of predation and competition. Oecologia 147, 744–753.

Fites-Kaufman, J., Rundel, P., Stephenson, N., Weixelman, D.A., 2007. Montane and subalpine vegetation of the Sierra Nevada and Cascade Ranges. In: Barbour, M.G., Keeler-Wolf, T., Schoenherr, A.A. (Eds.), Terrestrial vegetation of California, third edition. University of California Press, Berkeley, California, pp. 456–501.

Fontaine, J.J., Martel, M., Markland, H.M., Niklison, A.M., Decker, K.L., Martin, T.E., 2007. Testing ecological and behavioral correlates of nest predation. Oikos 116, 1887–1894.

Gabriel, M.W., Woods, L.W., Wengart, G.M., Stephenson, N., Higley, J.M., Thompson, C., Matthews, S.M., Sweitzer, R.A., Purcell, K.L., Barrett, R.H., Keller, S.M., Gaffney, P., Jones, M., Poppenga, R., Foley, J.E., Brown, R.N., Clifford, D.L., Sacks, B.N., 2015. Patterns of natural and human-caused mortality factors of a rare forest carnivore, the fisher (*Pekania pennanti*) in California. PLoS ONE 10, e0140640.

Gess, S.W., Ellington, E.H., Dzialak, M.R., Duchamp, J.E., Lovallo, M., Larkin, J.L., 2013. Rest-site selection by fishers (*Martes pennanti*) in the eastern deciduous forest. Wildl. Soc. Bull. 37, 805–814.

Gibilisco, C.J., 1994. Distributional dynamics of modern Martes in North America. Pp. 59–71 in Martens, sables, and fishers: biology and conservation (Buskirk, S.W., Harestad, A.S., Raphael, M.G., Powell, R.A., Eds.). Cornell University Press, Ithaca, New York.

Green, R.E., 2017. Reproductive ecology of the fisher (Pekania pennanti) in the Southern Sierra Nevada: an assessment of reproductive parameters and forest habitat used by denning females. Dissertation. University of California, Davis, California.

Green, R.E., Joyce, M.J., Matthews, S.M., Purcell, K.L., Higley, J.M., Zalewski, A, 2017. Guidelines and techniques for studying the reproductive ecology of wild fishers (Pekania pennanti), American martens (Martes americana), and other members of the Martes complex. Pp. 313–358 in The Martes Complex in the 21st century: ecology and conservation (Zalewski, A., Wierzbowska, I.A., Aubry, K.B., Birks, J.D.S., O'Mahony, D.T., Proulx, G., Eds.). Mammal Research Institute, Polish Academy of Sciences. Bialowieza, Poland.

Green, R.E., Purcell, K.L., Thompson, C.M., Kelt, D.A., Wittmer, H.U., 2018. Reproductive parameters of the fisher (*Pekania pennanti*) in the southern Sierra Nevada, California. J. Mammal. 99, 537–553.

Grinnell, J., Dixon, J.S., Linsdale, J.M., 1937. Fur-bearing mammals of California. Vol. 1. University of California Press, Berkeley, California.

Hankerson, S.J., Franklin, S.P., Dietz, J.M., 2007. Tree and forest characteristics influence sleeping site choice by golden lion tamarins. Am. J. Primatol. 69, 976–988.

Hennon, P.E., 1995. Are heart rot fungi major factors of disturbance in gap-dynamic forests? Northwest Sci. 69, 284–293.

Joyce, M.J., Zalewski, A., Erb, J.D., Moen, R.A., 2017. Use of resting microsites by members of the Martes complex: the role of thermal stress across species and regions. Pp. 181–220 in The Martes Complex in the 21st century: ecology and conservation (Zalewski, A., Wierzbowska, I.A., Aubry, K.B., Birks, J.D.S., O'Mahony, D.T., Proulx, G., Eds.). Mammal Research Institute, Polish Academy of Sciences. Bialowieza, Poland.

Kilpatrick, H.J., Rego, P.W., 1994. Influence of season, sex, and site availability on fisher (*Martes pennanti*) rest-site selection in the central hardwood forest. Can. J. Zool. 72, 1416–1419.

Laacke, R.J., Fiske, J.N., 1983. Red fir and white fir. Pages 41–43 in R. M. Burns, technical compiler. Silvicultural systems for the major forest types of the United States. Agricultural Handbook 445. U.S. Department of Agriculture, Forest Service, Washington D.C.

Laacke, R.J., 1990. Abies concolor (Gord. and Glend.) Lindl. ex Hildebr. White Fir. Pages 36–46 in R. M. Burns and B. H. Honkala, technical coordinators. Silvics of North America, Volume 1, Conifers. Agriculture Handbook 654. U.S. Department of Agriculture, Forest Service, Washington D.C.

Laliberte, A.S., Ripple, W.J., 2004. Range contractions of North American carnivores and ungulates. Bioscience 54, 123–138.

Lawton, K., Robertson, G., Kirkwood, R., Valencia, J., Schlatter, R., Smith, D., 2006. An estimate of population sizes of burrowing seabirds at the Diego Ramierez archipelago, Chile, using distance sampling and burrow-scoping. Polar Biol. 29, 229–238.

Lesmeister, D.B., Gompper, M.E., Millspaugh, J.J., 2008. Summer resting and den site selection by eastern spotted skunks (*Spilogale putorius*) in Arkansas. J. Mammal. 89, 1512–1520.

Lewis, J.C., Zielinski, W.J., 1996. Historical harvest and incidental capture of fishers in California. Northwest Sci. 70, 291–297.

Li, P., Martin, T.E., 1991. Nest-site selection and nesting success of cavity-nesting birds in high elevation forest drainages. Auk 108, 405–418.

Lofroth, E.C., Raley, C.M., Higley, J.M., Truex, R.L., Yaeger, J.S., Lewis, J.C., Happe, P.J., Finley, L.L., Naney, R.H., Hale, L.J., Krause, A.L., Livingston, S.A., Myers, A.M., Brown, R.N., 2010. Conservation of fishers (*Martes pennanti*) in south-central British Columbia, western Washington, western Oregon, and California-Volume 1: Conservation Assessment. USDI Bureau of Land Management, Denver, Colorado, USA.

Lutermann, H., Verburgt, L., Rendigs, A., 2010. Resting and nesting in a small mammal:

sleeping sites as a limiting resource for female gray mouse lemurs. Anim. Behav. 79, 1211–1219.
Mann, M.E., Gleick, P.H., 2015. Climate change and California drought in the 21st century. Proc. Natl. Acad. Sci. 112, 3858–3859. https://doi.org/10.1073/pnas.1503667112.
Manning, A.D., Gibbons, P., Fischer, J., Oliver, D.L., Lindenmayer, D.B., 2013. Hollow futures? Tree decline, lag effects and hollow-dependent species. Anim. Conserv. 16, 395–403.
Martin, K., Eadie, J.M., 1999. Nest webs: a community-wide approach to the management and conservation of cavity-nesting forest birds. For. Ecol. Manage. 115, 243–257.
Maser, C., Anderson, R.G., Cromack, K., Jr., Williams, J.T., Martin, R.E., 1979. Dead and down woody material. Pages 78–95 in Thomas, J.W. (Ed.). Wildlife habitats in managed forests-the Blue Mountains of Oregon and Washington. USDA Forest Service Agricultural Handbook 553.
Matthews, S.M., Higley, J.M., Rennie, K.M., Green, R.E., Goddard, C.A., Wengert, G.M., Gabriel, M.W., Fuller, T.K., 2013. Reproduction, recruitment, and dispersal of fishers (*Martes pennanti*) in a managed Douglas-fir forest in California. J. Mammal. 94, 100–108.
Matthews, S.M., Green, D.S., Higley, J.M., Rennie, K.M., Cummins, C.M., Green, R.E., In review. Reproductive den selection and its consequences for neonate survival of a cavity-obligate mustelid. J. Mammal.
Mayer, K.E., Laudenslayer, W.F., 1988. A guide to wildlife habitats of California. State of California, Resources Agency, Department of Fish and Game, Sacramento, CA. 166 pp. < https://www.wildlife.ca.gov/Data/CWHR/Wildlife-Habitats > .
Maziarz, M., Wesolowski, T., 2013. Microclimate of tree cavities used by great tits (*Parus major*) in a primeval forest. Avian Biol. Res. 6, 47–56.
McDonald, P.M., 1973. Incense cedar. Bulletin FS-226. U. S. Department of Agriculture, Forest Service, Washington D.C.
McDonald, P.M., 1990. Quercus kelloggii Newb., California black oak. Pages 661–671 in Burns, R.M. Honkala, B.H. (Eds.), Technical coordinators. Silvics of North America, Volume 2, Hardwoods. Agriculture Handbook 654. U. S. Department of Agriculture, Forest Service, Washington D.C.
McKelvey, K.S., Johnston, J.D., 1992. Historical perspectives on forests of the Sierra Nevada and the transverse ranges of southern California; forest conditions at the turn of the century. Chapter 11 in: Verner, J., McKelvey, K.S., Noon, B.R., Gutierrez, R.J., Gould, G.I., Beck, T.W. (Eds.), Technical Coordinators. The California spotted owl: a technical assessment of its current status. Gen. Tech. Rep. PSW-GTR-133. Albany, CA: Pacific Southwest Research Station, Forest Service, US Department of Agriculture; pp. 225–246.
Miller, C.I., Stephenson, N.L., 2015. Temperate forest health in an era of emerging megadisturbance. Science 349, 823–826.
NCSS 11 Statistical Software, 2016. NCSS, LLC. Kaysville, Utah, USA, ncss.com/software/ncss.
Oliver, C.D., Larson, B.C., 1996. Forest Stand Dynamics. John Wiley and Sons, Inc., New York.
Paragi, T.F., Arthur, S.M., Krohn, W.B., 1996. Importance of tree cavities as natal dens for fishers. Natl. J. Am. Forest. 13, 79–83.
Parsons, D.J., DeBenedetti, S.H., 1979. Impact of fires suppression on a mixed-conifer forest. For. Ecol. Manage. 2, 21–33.
Powell, R.A., 1993. The Fisher: Life History, Ecology, and Behavior. University of Minnesota Press, Minneapolis, Minnesota.
Powell, R.A., Leonard, R.D., 1983. Sexual dimorphism and energy expenditure for reproduction in female fisher *Martes pennanti*. Oikos 40, 166–174.
Powell, S.M., York, E.C., Scanlon, J.J., Fuller, T.K., 1997. Fisher maternal den sites in central New England. In: Proulx, G., Bryant, H.N., Woodard, P.M. (Eds.), *Martes*: taxonomy, ecology, techniques, and management. Provincial Museum of Alberta, Edmonton, Alberta, Canada, pp. 265–278.
Powell, R.A., Buskirk, S.W., Zielinski, W.J., 2003. Fisher and marten. In: Feldhamer, G.A., Thompson, B.C., Chapman, J.A. (Eds.), Wild Mammals of North America: Biology, Management, and Conservation. The Johns Hopkins University Press, Baltimore, Maryland, pp. 635–649.
Powers, R.F., Oliver, W.W., 1990. Incense-cedar. Pp. 173–180 in Burns, R.M., Honkala, B. H. (Eds.), tech. coordinators. Silvics of North America: 1. Conifers; Agriculture Handbook 654. U. S. Dept. of Agriculture, Forest Service, Washington, DC.
Purcell, K.L., Mazzoni, A.K., Mori, S.R., Boroski, B.B., 2009. Resting structures and resting habitat of fishers in the southern Sierra Nevada, California. For. Ecol. Manage. 258, 2696–2706.
R Core Development Team, 2015. R: a language and environment for statistical computing. R Foundation for Statistical Computing. Vienna, Austria. www.R-project.org.
Ranius, T., Kiklasson, M., Berg, N., 2009. Development of tree hollows in pedunculate oak (*Quercus robur*). For. Ecol. Manage. 257, 303–310.
Remm, J., Lõhmus, A., 2011. Tree cavities in forests – the broad distribution pattern of a keystone structure for biodiversity. For. Ecol. Manage. 262, 579–585.
Ross, S., Kamnitzer, R., Munkhtsog, B., Harris, S., 2010. Den-site selection is critical for Pallas's cats (*Otocolobus manul*). Can. J. Zool. 88, 905–913.
Ruggiero, L.F., Pearson, E., Henry, S.E., 1998. Characteristics of American marten den sites in Wyoming. J. Wildl. Manage. 62, 663–673.
Scholl, A.E., Taylor, A.H., 2010. Fire regimes, forest change, and self-organization in an old-growth mixed-conifer forest, Yosemite National Park, USA. Ecol. Appl. 20, 362–380.
Sikes, R.S., the Animal Care and Use Committee of the American Society of Mammalogists, 2016. 2016 Guidelines of the American Society of Mammalogists for the use of wild mammals in research and education. J. Mammal. 97, 663–688.
Slauson, K.M., Zielinski, W.J., 2009. Characteristics of summer and fall diurnal resting habitat used by American martens in coastal Northwestern California. Northwest Sci. 83, 35–45.
Taylor, S.L., Buskirk, S.W., 1994. Forest microenvironments and resting energetics of the American marten (*Martes americana*). Ecography 17, 249–256.
Tinnin, R.O., Hawksworth, F.G., Knutson, D.M., 1982. Witches' broom formation in conifers infected by *Arceuthobium* spp.: an example of parasitic impact upon community dynamics. Am. Midland Naturalist 107, 351–359.
Tinnin, R.O., Forbes, R.B., 1999. Red squirrel nests in witches' brooms in Douglas-fir trees. Northwestern Naturalist 80, 17–21.
Trousdale, J.W., Beckett, D.C., 2005. Characteristics of tree roosts of Rafinesque's big-eared bat (*Caorynorhinus rafinesquii*) in southeastern Mississippi. Am. Midland Naturalist 154, 442–449.
Truex, R.L., Zielinski, W.J., Golightly, R.T., Barrett, R.H., Wisely, S.M., 1998. A meta-analysis of regional variation in fisher morphology, demography, and habitat ecology in California. Draft report submitted to California Department of Fish and Game, Wildlife Management Division, Nongame bird and mammal section. 118 pp.
van Mantgem, P.J., Caprio, A.C., Stephenson, N.L., Das, A.J., 2016. Does prescribed fire promote resistance to drought in low elevation forests of the Sierra Nevada, California, USA? Fire Ecol. 12, 13–25.
Weir, R.D., Phinney, M., Lofroth, E.C., 2012. Big, sick, and rotting: Why tree size, damage, and decay are important to fisher reproductive habitat. For. Ecol. Manage. 265, 230–240.
Weir, R., Corbould, F., Harestad, A., 2004. Effect of ambient temperature on the selection of rest structures by fishers. In: Harrison, D.J., Fuller, A.K., Proulx, G. (Eds.), Martens and fisher (*Martes*) in human-altered environments: an international perspective. Springer Sciece + Business Media, New York, New York, pp. 187–197.
Wengart, G.M., Gabriel, M.W., Matthews, S.M., Higley, J.M., Sweitzer, R.A., Thompson, C.M., Purcell, K.L., Barrett, R.H., Woods, L.W., Green, R.E., Keller, S.M., Gaffney, P.M., Jones, M., Sacks, B.N., 2014. Using DNA to describe and quantify interspecific killing of fishers in California. J. Wildl. Manage. 78, 603–611.
Willis, C.K.R., Brigham, R.M., 2005. Physiological and ecological aspects of roost selection by reproductive female hoary bats (*Lasiurus cinereus*). J. Mammal. 86, 85–94.
Willis, C.K.R., Brigham, R.M., 2007. Social thermoregulation exerts more influence than microclimate on forest roost preferences. Behav. Ecol. Sociobiol. 62, 97–108.
Wisely, S.M., Buskirk, S.W., Russell, G.A., Aubry, K.B., Zielinski, W.J., 2004. Genetic diversity and structure of the fisher (*Martes pennanti*) in a peninsular and peripheral metapopulation. J. Mammal. 85, 640–648.
Wynne, K.M., Sherburne, J.A., 1984. Summer home range use by adult marten in northwestern Maine. Can. J. Zool. 62, 941–943.
Young, D.J.N., Stevens, J.T., Earles, J.M., Moore, J., Ellis, A., Jirka, A.L., Latimer, A.M., 2017. Long-term climate and competition explain forest mortality patterns under extreme drought. Ecol. Lett. 20, 78–86.
Zielinski, W.J., Truex, R.L., Schmidt, G.A., Schlexer, F.V., Schmidt, K.N., Barrett, R.H., 2004a. Resting habitat selection by fishers in California. J. Wildl. Manage. 68, 475–492.
Zielinski, W.J., Truex, R.L., Schmidt, G.A., Schlexer, F.V., Schmidt, K.N., Barrett, R.H., 2004b. Home range characteristics of fishers in California. J. Mammal. 85, 649–657.
Zielinski, W.J., Truex, R.L., Schlexer, F.V., Campbell, L.A., Carroll, C., 2005. Historical and contemporary distributions of carnivores in forests of the Sierra Nevada, California, USA. J. Biogeogr. 32, 1385–1407.