

BIOLOGY AND CONSERVATION OF

Martens, Sables, and Fishers

A New Synthesis

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Habitat Ecology of Fishers in Western North America

A New Synthesis

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ABSTRACT

In this chapter, we present a synthesis of the habitat associations of fishers (*Martes pennanti*) in western North America based on information produced since 1994. Contrary to limited results from previous studies, evidence from contemporary research indicates that fishers in western North America are not dependent on old-growth conifer forests for survival. Rather, fishers were associated with complex vertical (e.g., large trees and snags) and horizontal (e.g., large logs and dense canopy) structure characteristic of late-seral forests. Fisher distribution (first-order selection) was associated consistently with expanses of low- to mid-elevation mixed-conifer or conifer-hardwood forests with relatively dense canopies. Fisher home ranges (second-order selection) were characterized by a mosaic of available forest types and seral stages, including relatively high proportions of mid- to late-seral conditions, but low proportions of open or nonforested environments. Patterns of habitat use or selection by fishers were strongest at finer spatial scales (third- and fourth-order selection), and demonstrated that the fisher is a structure-dependent species in western North America. Female fishers are obligate cavity users for reproduction; tree cavities appeared to provide secure environments for kits by regulating temperature extremes and limiting access by predators. Compared with availability, fishers consistently selected large live trees, snags, and logs for resting that resulted from long-term forest growth and decay processes. Thermoregulation is more important to fishers than was recognized previously, and appeared to influence selection of rest structures and sites. Tree pathogens (e.g., heart-rot fungi, mistletoe) are essential for creating the microstructures used for reproduction (cavities) and resting (e.g., cavities, branch platforms), and represent important components of fisher habitat throughout the species' range in western North America. Our understanding of fisher habitat ecology has improved substantially since 1994. Nevertheless, focused investigations

of the mechanisms that may influence habitat selection by fishers at multiple spatial scales (especially at the home range scale) and correlating use or selection of environments to measures of individual fitness, are needed to better understand fisher habitat quality and improve the conservation and management of fisher populations in western North America.

Introduction

The geographic distribution of the fisher (*Martes pennanti*) in western North America (the Rocky Mountains west to the Pacific Ocean) has contracted substantially since European settlement, primarily as a result of overtrapping, predator control, and habitat loss through timber harvesting and other anthropogenic changes to forest landscapes (Powell and Zielinski 1994; Zielinski et al. 1995; Aubry and Lewis 2003; Lofroth et al. 2010). Although the commercial harvest of fishers has been closed for 6–20 years in southern British Columbia and >60 years in most other jurisdictions (Idaho, Washington, Oregon, California), and harvest limits have been reduced in Montana, fisher populations have not recovered in these portions of their historical range (U.S. Fish and Wildlife Service 2004, 2010; Lofroth et al. 2010).

Understanding the habitat relations of fishers and the influence of various environmental conditions on survival, reproduction, and other life needs is critical for the successful conservation of this species in western North America. The most recent synthesis of fisher habitat ecology was published almost 2 decades ago. In this comprehensive review, Buskirk and Powell (1994) hypothesized that the fisher was a habitat specialist and, in western North America, may require old-growth conifer forests for survival. Generally, the habitat associations of fishers were assumed to reflect those of their preferred prey, such as the snowshoe hare (*Lepus americanus*), which in the Pacific Northwest states coincided with the historical distribution of late-seral Douglas-fir forests (*Pseudotsuga menziesii*; Buskirk and Powell 1994). Evidence also suggested that fishers in western North America favored riparian forests. Overall, however, the structural characteristics of forest stands appeared more important to fishers than tree species composition (Buskirk and Powell 1994). These conclusions, also reflected in Powell and Zielinski's (1994) review of fisher ecology in the western United States, were based primarily on insights gained from fisher habitat studies conducted in eastern North America. Only 3 studies had been completed in the West prior to 1994: 1 telemetry study in northern California (Buck 1982; Buck et al. 1983, 1994), 1 detection study in northern California (Raphael 1984; Rosenberg and Raphael 1986), and 1 telemetry study in north-central Idaho (Jones 1991; Jones and Garton 1994). Although Powell and Zielinski (1994) included details in

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their review from 2 ongoing telemetry studies in northern California, research on fisher populations in the West was still in its infancy. Since 1994, numerous field studies on fisher habitat ecology in British Columbia, Montana, Idaho, Oregon, and California have been conducted or are currently in progress (Lofroth et al. 2010).

Our objectives in this chapter are (1) to identify new advances in our understanding of fisher habitat ecology since 1994, (2) to synthesize key findings and compare them with previous understandings of fisher habitat relations, and (3) to identify key information gaps and new avenues for research that would benefit conservation efforts and habitat management for this species in western North America. In this chapter, we relied extensively on the detailed literature review and data summaries of fisher habitat associations we presented in Lofroth et al. (2010) and do not repeat those details here. Rather, this chapter is a synthesis of the overarching patterns that emerged during that review; patterns that represent key components of fisher habitat, fisher life needs, and other factors that influence the habitat choices fishers make. We have presented these patterns in the order of their perceived importance to fishers based on our evaluations, beginning with the strongest and most consistent patterns, which also reflects a gradient of increasing spatial scale. We then summarize our key findings within the context of hierarchical habitat use or selection by fishers in western North America.

Fisher Habitat Studies

We reviewed 18 published papers and 24 unpublished reports, dissertations, or theses from 23 geographic areas in western North America that presented results on fisher habitat use or selection at various spatial scales (Table 10.1). This body of literature represents new information on fisher habitat ecology generated from 1994 through 2010. We also included 1 dataset (Simpson Resource Company, unpublished data) that augmented information presented in Thompson et al. (2007). For ongoing studies that produced progress reports (e.g., Thompson et al. 2010), we included relevant data on the characteristics of forest environments used by fishers, but not results from interim analyses of resource selection. Information on fisher habitat ecology was available for all geographic areas in western North America in which extant fisher populations occur (Figure 10.1), but more studies have been conducted in northern California and the southern Sierra Nevada than elsewhere. For detailed summaries of the individual field studies that produced information on fisher habitat ecology, including objectives, duration of field sampling, and methods, we refer readers to Lofroth et al. (2011). In the Rocky Mountain region, 2 telemetry studies, 1 in north-central Idaho (J. Sauder, Idaho Department of Fish and Game, personal communication) and 1 in west-central Montana

Table 10.1. Information on fisher habitat ecology in western North America produced from 1994 through 2010

Geographic area	Published	Unpublished	Method and order of selection
Pacific coastal provinces and states			
Regional			
Central British Columbia	Weir and Corbould 2010	Buskirk et al. 2010	T, 3
Williston Reservoir	Weir et al. 2004		T, 2 T, 4
		Weir and Corbould 2008	T, 2-4
McGregor	Proulx 2006a		S, 3
Chilcotin		Calabrese and Davis 2010	n/a ^a , 4
		Davis 2003	S, 3
		Davis 2009	T, 2-4
Beaver Valley	Weir and Harestad 1997		T, 3
	Weir and Harestad 2003		T, 3-4
	Weir et al. 2004		T, 4
Rocky Mountain provinces and states			
Regional			O, 1
Southern Oregon	Carroll et al. 2001		
Cascade Range		Aubry and Raley 2006	T, 3-4
Siskiyou National Forest		Slauson and Zielinski 2001	D, 3
Northern California			
Regional			
	Carroll et al. 1999		D, 1, 3
	Carroll et al. 2010		D, 1
	Davis et al. 2007		D, 1
	Zielinski et al. 2010		D, 1
	Thompson et al. 2007	Carroll 2005a	D, 1 T, 4
Coastal region			
		Beyer and Golightly 1996	D, 1, 3
		Klug 1997	D, 1, 3
Redwood National and State Parks		Slauson and Zielinski 2003	D, 1, 3
Hoop Valley Indian Reservation		Higley and Matthews 2009	T, 2-4
		Yaeger 2005	T, 3-4

Southern Oregon			
Cascade Range			T, 3-4
Siskiyou National Forest		Aubry and Raley 2006	D, 3
Northern California		Slauson and Zielinski 2001	
Regional			
	Carroll et al. 1999		D, 1, 3
	Carroll et al. 2010		D, 1
	Davis et al. 2007		D, 1
	Zielinski et al. 2010		D, 1
Coastal region	Thompson et al. 2007	Carroll 2005a	D, 1
			T, 4
		Beyer and Golightly 1996	D, 1, 3
Redwood National and State Parks		Klug 1997	D, 1, 3
Hoopla Valley Indian Reservation		Slauson and Zielinski 2003	D, 1, 3
		Higley and Matthews 2009	T, 2-4
		Yaeger 2005	T, 3-4
			T, 4
			D, 3
Pilot Creek, Six Rivers National Forest	Zielinski et al. 2004a		T, 3-4
	Zielinski et al. 2004b		T, 2
Sacramento Canyon		Truex et al. 1998	T, 3-4
		Reno et al. 2008	T, 4
Shasta Trinity National Forest		Self and Kerns 2001	T, 2-4
		Dark 1997	T, 3; D, 1, 3
		Seglund 1995	T, 3-4
		Yaeger 2005	T, 3-4
Hayfork Summit		Reno et al. 2008	T, 4
Mendocino National Forest		Slauson and Zielinski 2007	
Sierra Nevada, California			
Regional			
	Carroll et al. 2010		D, 1
	Davis et al. 2007		D, 1
	Spencer et al. 2011		D, 1
Yosemite National Park		Campbell 2004	D, 1, 3
Kings River, Sierra National Forest	Chow 2009		O, 1
	Purcell et al. 2009		T, 3-4
	Thompson et al. 2011		T, 2
	Zielinski et al. 2006c		T, 3
Blodgett Forest and Sequoia National Park		Mazzoni 2002	T, 2-4
Sequoia and Kings Canyon National Parks		Thompson et al. 2010	T, 4
Tule River, Sequoia National Forest		Truex and Zielinski 2005	T, 3; D, 3
		Green 2007	D, 1
	Zielinski et al. 2004a		T, 3-4
	Zielinski et al. 2004b		T, 2
	Zielinski et al. 2006c		T, 3
		Truex et al. 1998	T, 3-4

Note: To determine fisher presence or use, investigators of fisher habitat ecology used telemetry (T), detection methods using track-plates or remotely triggered cameras (D), snow tracking (S), or occurrence data from museum specimens, trapping records, and sighting reports (O). Many studies investigated fisher habitat ecology at >1 order of selection: (1) first order, geographic distribution; (2) second order, home range; (3) third order, environments within a home range; and (4) fourth order, specific resources within an environment. Geographic areas are presented by latitude from north to south and, for California, from the coast inland; some sources apply to >1 geographic area.

^a Study sampled potential reproductive den structures but did not sample fisher presence or use

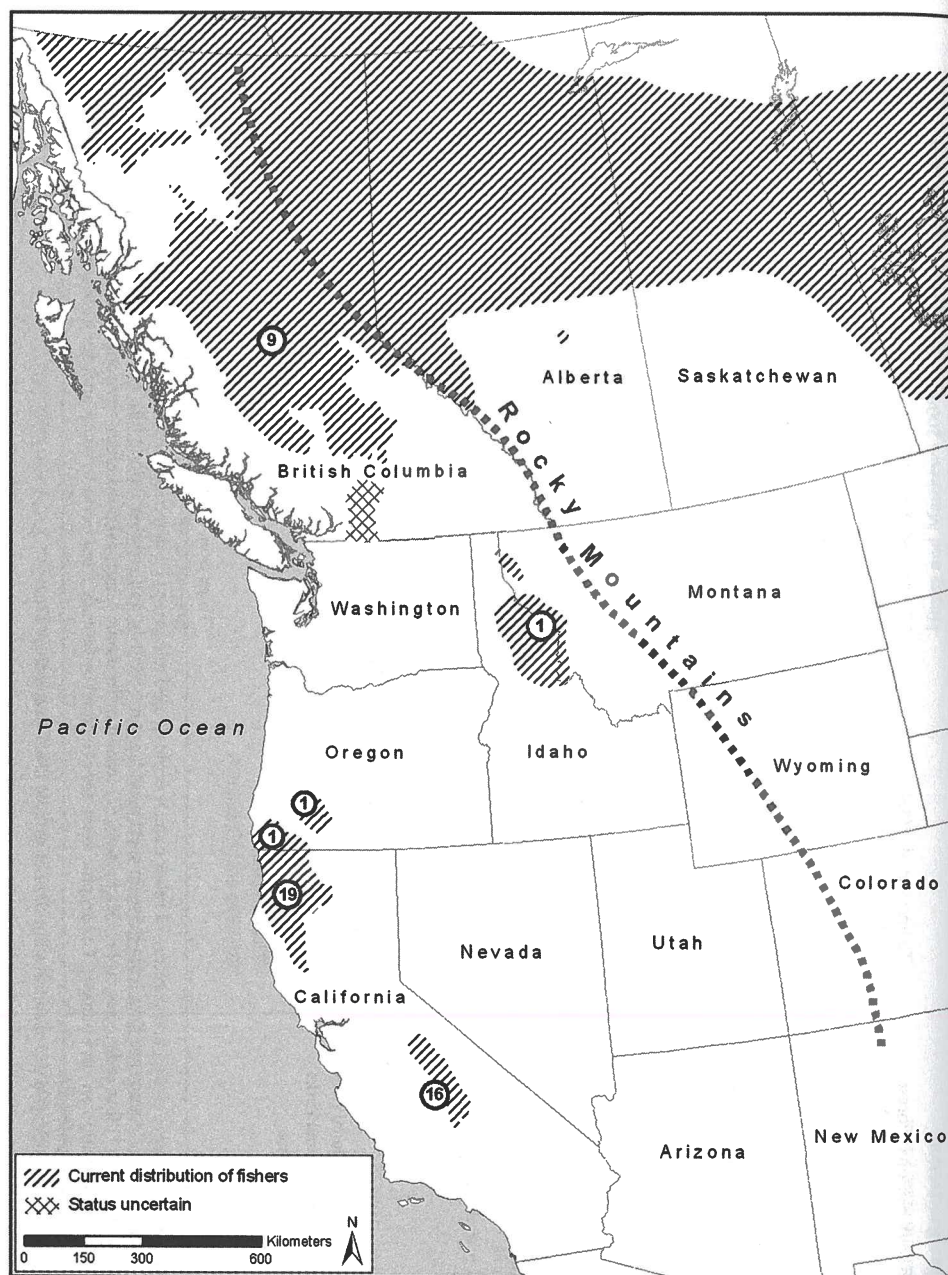


Figure 10.1. Number of published and unpublished sources of information on fisher habitat ecology in western North America produced from 1994 to 2010. Some sources generated information for >1 region. Map does not include 1 regional source that applies to British Columbia, Oregon, and California (Buskirk et al. 2010). Current distribution of fishers is based on Lofroth et al. (2010).



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(M. Schwartz, USDA Forest Service, personal communication), were completed, but the results were not available at this time.

For this synthesis, we have focused on the habitat ecology of established fisher populations in western North America, including both indigenous and reintroduced populations. Although we recognize the value of investigating the habitat associations of recently translocated fishers in British Columbia (e.g., Fontana et al. 1999), Washington (Lewis et al. 2011), and California (Callas and Figura 2008), we have not included information from such studies here. Translocated animals are naïve to their new environment and may not yet have learned which habitat conditions are available or provide the best suite of resources to meet their life needs, such as escape from predators, foraging, resting, and reproduction.

Fishers select habitat at multiple spatial scales for different activities or behaviors (Powell and Zielinski 1994; Weir and Harestad 1997). First-order selection determines a species' geographic distribution; second-order, selection or composition of individual home ranges within that distribution; third-order, selection or use of different environments within a home range (e.g., stand types, rest sites); fourth-order, selection or use of specific resources within those environments (e.g., rest structures, food items; see Johnson 1980). We were mindful of these concepts in our evaluations, and the conclusions and hypotheses we present are based on interpreting available evidence at appropriate and comparable spatial scales. Although many fisher studies investigated habitat use or selection at multiple spatial scales, third- and fourth-order studies were most prevalent (Table 10.1).

Investigators of fisher habitat ecology use various terminologies to describe the characteristics of environments or resources used by their study animals. In this synthesis, we use the term *habitat* to indicate the suite of resources or environmental conditions that meet the life needs of fishers. The terms *selection* and *preference* are often used interchangeably in the literature, but selection refers to the process of choosing resources, whereas preference is the likelihood an animal will choose a resource, given the equal availability of other resources (Johnson 1980). Hence, we use the term *selection* when use of a resource was demonstrated to be greater or less than its availability. Investigators have measured forest canopy in different ways, and it was not always possible to determine which attributes of the canopy had been measured (e.g., canopy cover by trees vs. all overhead vegetation). Thus, we use the term *canopy cover* to represent all such measurements, and then provide additional clarification as needed. The term *forest structure* refers to numerous components that contribute to the vertical and horizontal complexity of forests, including distributions of tree sizes and ages, standing and down dead wood, vertical foliage distribution (understory and overstory vegetation layers), and horizontal canopy distribution (e.g., Spies 1998). The term *structure* refers to a live tree, snag (dead tree), or log (including all coarse

down wood) used by a fisher, whereas the term *microstructure* refers to various features within the structures, such as a mistletoe broom in a live tree, cavity in a snag, or hollow in a log. Descriptions of the *sites* used by fishers for resting or denning include the rest or den structure and the forest conditions measured in the immediate vicinity of that structure (typically <0.5 ha). Finally, to provide meaningful insights on denning ecology, we categorized dens used by reproductive females according to the developmental stage of the kits (see Lofroth et al. 2010): (1) *natal dens* are the tree cavities in which parturition occurs; (2) *pre-weaning dens* are any subsequent structure used after the natal den but before the kits are weaned; (3) *post-weaning dens* are any structure used after the kits are weaned; and (4) *reproductive dens* refer to all dens used by an adult female during a single reproductive effort, or when the developmental stage of the kits was unknown.

Importance of Forest Structure at Small Spatial Scales

Den Structures

An extensive body of literature demonstrates that the fisher is a structure-dependent species in western North America. Reproductive females are obligate cavity users; they use cavities in large-diameter live trees and snags exclusively for birthing and rearing kits until weaning. Fisher kits are born during the late winter and early spring when weather conditions are cold and wet. Because kits are altricial at birth, and their ear canals and eyes remain closed until about 8 weeks of age (Powell 1993), we conclude that tree cavities are essential components of fisher habitat that provide thermoregulatory advantages to kits and protect them from predators.

With the exception of 2 reproductive dens in California and 1 in Idaho (Powell and Zielinski 1994), little was known about fisher denning habitat in western North America prior to 1994. New information from >330 reproductive dens in 12 geographic areas, however, has greatly improved our understanding of fisher denning ecology. In most cases, the cavities that reproductive female fishers used for natal and pre-weaning dens were created by heartwood decay through the action of heart-rot fungi (e.g., Aubry and Raley 2006; Reno et al. 2008; Weir and Corbould 2008). Most post-weaning dens were also in tree cavities, although females with older kits occasionally used other types of structures, including hollow logs (Aubry and Raley 2006). Reproductive den trees were always among the largest trees available; 1.7–2.8 times larger in diameter on average than other trees in the vicinity of the den (e.g., Reno et al. 2008; Weir and Corbould 2008; Davis 2009). Trees used for denning were old; the average estimated age of reproductive den trees in British Columbia was 372 years for Douglas-fir, 177 years for lodgepole pine (*Pinus contorta*), and 96 years for trembling aspen (*Populus tremuloides*;

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Davis 2009). Typically older (thus, larger diameter) trees have a higher inci-
dence of heartwood decay than younger trees (Manion 1991). In some re-
gions, conifers were used for denning more than hardwoods (e.g., Aubry and
Raley 2006; Davis 2009; Thompson et al. 2010), whereas, in other regions,
hardwoods were used more frequently even if they were a minor component
of the forest (e.g., Weir and Harestad 2003; Weir and Corbould 2008; Higley
and Matthews 2009). However, available evidence indicates that the inci-
dence of heartwood decay and cavity development is more important to fish-
ers for denning than is the tree species.

Other characteristics, such as the size and height of the cavity opening and
the interior dimensions of the cavity, may also influence females' choice of
natal and pre-weaning den structures. The cavity must be large enough to ac-
commodate an adult female and 1–4 growing kits, and have a relatively small
opening (just large enough for a female to fit through) high off the ground
(15–26 m on average; e.g., Aubry and Raley 2006; Weir and Corbould 2008;
Thompson et al. 2010). These characteristics may be important for excluding
potential predators and aggressive male fishers. During the breeding season,
adult males locate a natal den and wait for an opportunity to mate with the
female when she exits the cavity (Lofroth et al. 2010); the relatively small cav-
ity opening may prevent males from entering the cavity and injuring or killing
the kits. Consequently, the large diameter of structures used for denning may
reflect the age of the tree, the presence of heartwood decay, and the need for a
large and structurally sound interior chamber in the mid- to upper bole,
where most natal and pre-weaning dens are located. Presumably, the cavity
must also have adequate thermal properties to protect kits from weather ex-
tremes. Compared with ambient temperatures, tree cavities provide stable
microclimates with narrow temperature fluctuations (Sedgeley 2001; Weir
and Corbould 2008; Coombs et al. 2010). Most (75%) of the dens used by
reproductive female fishers were in live trees. Cavities in relatively large live
trees appear to have more stable temperatures during the day, and stay warmer
at night, than those in relatively small snags (Wiebe 2001; Coombs et al.
2010). Other factors, such as the orientation of the cavity and exposure to
sunlight (i.e., amount of canopy cover), may also influence the thermal prop-
erties of cavities, but quantitative evidence is lacking.

Rest Structures and Sites

Fisher resting habitat in western North America is also strongly tied to
forest structure. Fishers typically rest in large deformed or deteriorating live
trees, snags, and logs, and forest conditions around the rest structures (i.e.,
the rest site) frequently include structural elements characteristic of late-seral
forests. Although this generally agrees with previous descriptions of fisher
resting habitat (Buskirk and Powell 1994; Powell and Zielinski 1994), we now

have evidence from >2260 rest structures from 12 different geographic areas (compared with <200 rest structures from 2 areas prior to 1994) that the characteristics of structures used by fishers for resting are overwhelmingly consistent throughout western North America.

Fishers rested primarily in deformed or deteriorating live trees (54–83% of all rest structures identified in individual studies), and secondarily in snags (6–26%) and logs (3–20%; e.g., Weir and Harestad 2003; Zielinski et al. 2004b; Aubry and Raley 2006; Purcell et al. 2009). The species of trees and logs used for resting appeared to be less important than the presence of cavities, platforms, and other microstructures. In live trees, fishers rested primarily in rust brooms in more northern study areas (Weir and Harestad 2003; Weir and Corbould 2008; Davis 2009) and mistletoe brooms or other platforms elsewhere (e.g., Self and Kerns 2001; Yaeger 2005; Aubry and Raley 2006). In contrast, fishers primarily used cavities when resting in snags (e.g., Self and Kerns 2001; Zielinski et al. 2004b; Purcell et al. 2009). Fishers used hollow portions of logs or subnivean spaces beneath logs more frequently in regions with cold winters (e.g., Weir and Harestad 2003; Aubry and Raley 2006; Davis 2009) than those with milder winters (e.g., Yaeger 2005; Purcell et al. 2009; Thompson et al. 2010). These results suggest that fishers use structures associated with subnivean spaces to minimize heat loss during cold weather (Weir et al. 2004; Weir and Corbould 2008). Many of the microstructures fishers need are created through the actions of particular organisms (e.g., rust fungi, heart-rot fungi) or ecological conditions (e.g., tree species in decline) and take decades to develop. Because fishers frequently rest in cavities in large trees or snags (similar to structures used for denning), a suitable microstructure may require >100 years to develop. Live trees, snags, and logs used for resting were, on average, 1.4–3.4 times larger in diameter than available structures (e.g., Weir and Harestad 2003; Zielinski et al. 2004b; Purcell et al. 2009). The large size of these structures is likely related to tree age and the long time periods required for various microstructures to develop.

Forest conditions around rest structures also influence a fisher's choice of rest sites. Compared with available sites, those used by fishers for resting had ≥ 1 of these structural components: greater average tree diameter or greater abundance of large-diameter trees, presence of large-diameter snags or greater abundance of snags, greater average size of logs or greater abundance of logs (primarily British Columbia and Oregon studies), and greater average diameter or greater abundance of hardwood trees (primarily California studies) (e.g., Zielinski et al. 2004b; Davis 2009; Purcell et al. 2009). A meta-analysis that included data from 8 studies in British Columbia, Oregon, and California confirmed this general pattern and demonstrated that, throughout the West, fishers consistently select sites for resting that have larger diameter conifer and hardwood trees, larger diameter snags, more abundant large trees and snags, and more abundant logs than random sites (Buskirk et al. 2010).

Several hypotheses have been proposed to explain these patterns. Because deteriorating trees, snags, and logs tend to be patchy in distribution (Bull et al. 1997), fishers may expend less energy finding suitable rest structures by selecting sites with a greater abundance of potential structures from which to choose (e.g., Seglund 1995; Weir and Corbould 2008; Davis 2009). A hardwood component in rest-site selection models for the Sierra Nevada was believed to represent the importance of black oaks (*Quercus kelloggii*) to fishers for rest structures (Zielinski et al. 2004b). An abundance of nearby large trees may also create favorable microclimates for resting fishers, especially in hotter and drier regions (Zielinski et al. 2004b; Purcell et al. 2009). Others have speculated that greater abundance or size of structures, or prevalence of hardwoods (especially mast-producing species), may reflect sites with more abundant prey (e.g., Yaeger 2005; Davis 2009; Purcell et al. 2009), thus providing energetic benefits for foraging. Rest sites with a relatively high density of large structures may also provide fishers with escape cover and protection from predators. We believe these are all plausible hypotheses and propose that, although rest sites may not be as clearly linked to fitness as reproductive den sites, they provide fishers with multiple advantages that improve individual fitness (e.g., thermal, security, and proximity to prey).

Forest Structure Associated with Active Fishers

When engaged in active behaviors (e.g., foraging, traveling), fishers in western North America were frequently associated with complex forest structure. In general, active fishers were associated with the presence, abundance, or a greater size of ≥ 1 of the following characteristics: logs, snags, live hardwood trees, and shrubs (e.g., Carroll et al. 1999; Slauson and Zielinski 2003; Weir and Harestad 2003; Campbell 2004). Although these results indicate that complex vertical and horizontal structure is important to active fishers, we did not find strong overarching patterns of use or selection. Some have suggested that the environments used by active study animals reflect foraging habitat (e.g., Buskirk and Powell 1994), but this idea has not been evaluated critically. Most methods used to study fisher habitat ecology (e.g., telemetry, noninvasive techniques) do not allow the investigator to distinguish among active behaviors such as foraging, traveling, seeking mates, or dispersal. Thus, the lack of strong habitat-association patterns for active fishers may reflect the sampling of multiple behaviors, each of which could be linked to different forest conditions. Alternatively, if the behavior sampled is primarily foraging, the lack of consistent patterns could reflect the diverse diets of fishers (e.g., Zielinski et al. 1999; Weir et al. 2005; Aubry and Raley 2006) and varying habitat associations among prey species, or the forest conditions in which fishers are most effective at capturing prey (see Buskirk and Powell 1994). Regardless,

more-focused investigations are needed to understand the habitat associations of active fishers and the relations between fishers and their prey. Improved sampling methods that enable investigators to better distinguish among active behaviors would benefit such efforts.

Importance of Tree Pathogens for Creating Den and Rest Structures

Fisher habitat in western North America is intricately linked to a complex web of ecological processes that include natural disturbances (e.g., wind, fire), tree pathogens, and other organisms (e.g., primary excavators) that create and influence the distribution and abundance of microstructures (e.g., cavities, mistletoe brooms) in live trees, snags, and logs. Because female fishers rely exclusively on tree cavities for reproduction, we conclude that heartwood decay by heart-rot fungi, the process by which most reproductive den cavities are created, is an essential component of fisher denning habitat in western North America. This ecological process is also important for creating the microstructures that fishers use for resting (cavities in live trees and snags, and hollows in logs).

Heartwood decay by heart-rot fungi (specialized fungi that can tolerate the chemical defenses of live trees) is a complex process that can be initiated only in living trees (Manion 1991; Bull et al. 1997). Consequently, for live trees, snags, or logs to contain the types of cavities or hollows needed by fishers for denning and resting, heart-rot fungi must infect a live tree and persist long enough to decay a sufficiently large core of heartwood before the tree dies. Older, suppressed, or unhealthy trees are less capable of responding to injuries and defending themselves against infection by heart-rot fungi than are younger or healthier trees (Wagener and Davidson 1954; Manion 1991). Thus, advanced tree age and environmental stressors are important factors contributing to the susceptibility of live trees to infection by heart-rot fungi (Wagener and Davidson 1954; Manion 1991) and, consequently, the development of suitable cavities for fishers. Compared with conifers, hardwoods typically have thinner bark and their open growth form make them more susceptible to breakage (Gumtow-Farrior 1991; Bunnell et al. 2002). Hence, relatively young hardwood trees may have higher rates of infection by heart-rot fungi than similarly aged conifers. Nevertheless, for any tree to provide a cavity large enough for a fisher to use, decades are required for the tree to attain a large diameter, for damage or other stress factors to weaken its vigor, and for heartwood decay to reach an advanced stage and develop a suitable cavity.

Several investigators have reported fishers commonly using pileated woodpecker (*Dryocopus pileatus*) cavities as natal or pre-weaning dens (Aubry and Raley 2006; Reno et al. 2008; Davis 2009; Higley and Matthews 2009). This primary excavator creates a relatively large nest cavity in live trees or snags

understand the habitat associations of fishers and their prey. Improved ability to better distinguish among active

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intricately linked to a complex of disturbances (e.g., wind, fire), many excavators) that create and modify microstructures (e.g., cavities, logs). Because female fishers rely on these, we conclude that heartwood decay is the most reproductive den cavities and the best denning habitat in western North America. It is important for creating the microstructures in live trees and snags, and

specialized fungi that can tolerate decay is a process that can be initiated (Davidson 1997). Consequently, for live trees, cavities or hollows needed by fishers are more likely to be infected and persist in live trees than in heartwood before the tree is removed. It is less capable of responding to infection by heart-rot fungi than in live trees (Davidson 1954; Manion 1991). Disturbances are important factors that contribute to infection by heart-rot fungi and, consequently, the development of heart-rot in conifers, hardwoods, and snags make them more susceptible to infection (Schnell et al. 2002). Hence, rates of infection by heart-rot fungi are high, for any tree to provide a cavity that is required for the tree to attain a suitable resting habitat to weaken its vigor, and to develop a suitable cavity. Commonly using pileated woodpeckers for pre-weaning dens (Aubry and Raley 2002b; Aubry and Matthews 2009). This is the best cavity in live trees or snags

that have been softened by heartwood decay and, for roosting, excavates openings into portions of trees that have been hollowed out by advanced decay (Bull et al. 1992; McClelland and McClelland 1999; Aubry and Raley 2002a). In addition, through both cavity and foraging excavations, woodpeckers may facilitate the inoculation of live trees with heart-rot fungi (e.g., Aubry and Raley 2002b). Thus, in some regions, pileated woodpeckers may benefit fishers by initiating heartwood decay in live trees that will eventually create cavities that fishers can use for denning, or by providing fishers with access to naturally formed tree cavities that did not previously have an opening.

In each locality, forest management likely influences which tree species may become infected by heart-rot fungi and develop potential den and rest structures for fishers. Tree species managed for timber production (primarily conifers in western North America) are generally harvested before they reach older age-classes and become more susceptible to infection by heart-rot fungi. In contrast, species not managed for timber production (primarily hardwood species, but also conifer species without a high market value) are more likely to reach older ages and be exposed to various stressors that contribute to infection by heart-rot fungi. Some management practices retain older or deteriorating trees in leave patches or buffer zones (e.g., stream or riparian buffers). In this context, both conifer and hardwood species may have a higher incidence of decay by heart-rot fungi than do the same species in stands managed for timber production. Furthermore, if leave patches or buffer zones are permanent features on the landscape, the younger trees retained in these areas provide for future recruitment of older trees with heartwood decay.

Brooming or platforms in live trees caused by parasitic plants such as dwarf mistletoes (*Arceuthobium* spp.) or rust fungi (*Chrysomyxa* spp. or *Melampsorella* spp.), and the development of branch platforms in older trees, are additional ecological processes that are important for creating and maintaining fisher resting habitat in western North America. Because dwarf mistletoes and rust fungi can have a negative impact on timber production (i.e., tree deformities, stunted growth, and mortality [especially dwarf mistletoes]; Scharpf 1993; Allen et al. 1996; Parks and Bull 1997), infected trees are frequently removed to control or eradicate these pathogens from a stand. Consequently, some forest-management practices can interrupt these ecological processes and decrease the availability of microstructures that provide suitable resting habitat for fishers.

A better understanding of how these key processes function would provide valuable insights about regional variation in the availability of denning and resting habitat, and the ways in which fisher habitat may shift over time in response to disturbance events or changes in forest-management strategies. Also, few researchers have estimated the age of trees used for denning or resting (Davis 2009). Determining the ages of den and rest trees would improve

our understanding of the time periods needed for these ecological processes to create suitable microstructures and, consequently, how forest managers can best maintain or promote them to benefit fishers.

Importance of Rest Structures and Sites for Thermoregulation

The need to minimize heat loss during cold weather is more important to fishers than was recognized previously. Buskirk and Powell (1994) speculated that, because of their larger size, thermal losses while resting are not as important for fishers as they are for American martens (*M. americana*), and access to subnivean spaces did not appear to influence their choice of resting habitat during winter. Although the metabolic demands and energetic constraints experienced by these 2 species during winter may differ, new evidence indicates that fishers in western North America select rest structures during cold weather that provide them with thermal benefits.

The strongest evidence that thermoregulatory constraints influence habitat selection by fishers comes from studies conducted in the northern part of their range in western North America. In British Columbia, fishers primarily used arboreal structures (branch platforms and cavities in trees) for resting throughout the year, but switched to logs or other ground structures (e.g., middens, burrows) when temperatures dropped and the snow pack was deep enough to provide subnivean spaces (Weir and Corbould 2008; Davis 2009). Fishers were most likely to select subnivean spaces associated with logs rather than arboreal structures for resting when ambient temperatures fell below -11°C (Weir and Corbould 2008), and used subnivean spaces exclusively when temperatures were colder than -15°C (Weir et al. 2004; Weir and Corbould 2008). Although other studies have not measured the temperature or precipitation regimes associated with the use of different rest structures by fishers, there is a general pattern of greater use of ground structures in regions that have colder winters (19–39% of all rest structures in British Columbia and the Cascade Range of Oregon; e.g., Weir and Harestad 2003; Aubry and Raley 2006; Davis 2009) than in those with milder winters (2–10% of rest structures in California; e.g., Zielinski et al. 2004b; Yaeger 2005; Purcell et al. 2009).

Available evidence also indicates that selection of rest sites by fishers in western North America may be influenced by their need for thermal relief during hot weather. Several investigators have hypothesized that, in the hotter and drier portions of their range (e.g., southern Sierra Nevada in California), selection by resting fishers for steep slopes, dense canopy cover, and proximity to water represents selection for cool sites and favorable microclimates (Zielinski et al. 2004b; Purcell et al. 2009). Although no data were available for warmer regions, there is evidence that the types of microstructures used by

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for these ecological processes to eventually, how forest managers can address them.

Whether it is more important to fishers or not, and Powell (1994) speculated that while resting are not as important as for martens (*M. americana*), and can influence their choice of resting sites. Climatic demands and energetic constraints may differ, new evidence suggests that fishers select rest structures during winter months for benefits.

Environmental constraints influence habitat selection. Conducted in the northern part of British Columbia, fishers primarily used cavities in trees for resting sites, rather than other ground structures (e.g., logs, snow, and the snow pack was deep in the Corbould 2008; Davis 2009). In spaces associated with logs when ambient temperatures fell below 5°C (Weir et al. 2004; Weir and Davis 2005) not measured the temperature of different rest structures by type of ground structures in regions of British Columbia and Harestad 2003; Aubry and Davis 2004; Jaeger 2005; Purcell 2005).

Selection of rest sites by fishers is influenced by their need for thermal relief. We hypothesized that, in the hotter regions of Sierra Nevada in California, fishers use canopy cover, and proximity to favorable microclimates (Zielinski et al. 2004a). Although no data were available for the types of microstructures used by

fishers for resting during hot weather (e.g., branch platforms, cavities in trees or snags) may also be influenced by thermoregulatory needs. We hypothesize that selection of rest structures and sites by fishers is influenced, in part, by their need to maintain thermoneutrality during both cold and hot weather to minimize their energetic costs. Focused investigations are needed to determine whether these patterns are consistent throughout western North America, or if they are pronounced only in regions that experience more extreme temperature or precipitation conditions. To elucidate the importance of thermoregulatory constraints on fishers, we recommend that future studies include focused sampling during periods of temperature and precipitation extremes, rather than simply comparing differences among seasons, which could mask important influences on resting habitat selection by fishers.

Importance of Canopy Cover at Multiple Spatial Scales

In western North America, a moderate to dense forest canopy is one of the strongest and most consistent predictors of fisher distribution and habitat use or selection at all spatial scales. The association of fishers with high amounts of canopy cover is further demonstrated by their avoidance of open environments. Early studies in the West indicated that canopy cover was important to fishers, but avoidance of areas with no tree or shrub cover was a more consistent pattern (Buskirk and Powell 1994; Powell and Zielinski 1994). Nevertheless, specific information on these associations at different spatial scales was lacking, and the biological significance of canopy cover to fishers was unclear. Based on the wealth of information now available, we conclude that moderate-to-dense canopy cover is a critical component of fisher habitat throughout western North America that is linked to multiple aspects of the fisher's life needs.

At regional and landscape scales, an increasing amount of forest canopy was the most consistent predictor of fisher occurrence in California (Carroll et al. 1999; Carroll 2005a; Davis et al. 2007; Zielinski et al. 2010). Similarly, fisher occurrence in the Rocky Mountain region was positively correlated with canopy cover up to an apparent threshold of 60% (Carroll et al. 2001). Fisher home ranges included primarily forests with moderate-to-high canopy-cover values for the region being studied. In British Columbia, fishers selected home ranges with $\geq 30\%$ canopy cover (Weir and Corbould 2010). In the Sierra Nevada, one study showed mean canopy cover of 63% within female home ranges (Thompson et al. 2011), whereas another reported that 66% of the area within all fisher home ranges was composed of the densest (60–100%) canopy-cover class (Zielinski et al. 2004a). Fishers avoided open areas when selecting home ranges in British Columbia (Weir and Corbould 2010) and, in California, the average proportion of fisher home ranges that included open environments was $\leq 5\%$ (Self and Kerns 2001; Zielinski et al. 2004a;

Higley and Matthews 2009). At smaller spatial scales, fishers selected sites for resting that had denser canopies than random sites (e.g., Zielinski et al. 2004b; Davis 2009; Purcell et al. 2009). The generality of this association throughout the West was confirmed by a meta-analysis of rest-site selection that included data from 8 study areas in British Columbia, Oregon, and California (Buskirk et al. 2010).

Previously, it was thought that the positive association of fishers with canopy cover (and their avoidance of open areas) was related to predator avoidance, but Buskirk and Powell (1994) noted that little evidence existed of predation on fishers to support that hypothesis. However, recent studies have demonstrated that predation on fishers in western North America is relatively common; documented predators included bobcat (*Lynx rufus*), cougar (*Puma concolor*), Canada lynx (*Lynx canadensis*), coyote (*Canis latrans*), and wolverine (*Gulo gulo*) (Truex et al. 1998; Weir and Corbould 2008; Higley and Matthews 2009); predation by raptors appears to be uncommon (e.g., Truex et al. 1998). Thus, it seems likely that selection for relatively dense canopies by fishers is explained, at least in part, by the vertical escape cover (i.e., tree boles) they provide from terrestrial predators (e.g., Weir and Corbould 2010). Forests with greater amounts of canopy cover are also likely to provide more favorable microclimatic conditions for fishers. The amount and structure of forest canopies have a profound influence on microclimates, including absorption of solar radiation (Spies 1998) and interception of snowfall, which affects snow-accumulation patterns (Storck et al. 2002). Recent studies have demonstrated that thermoregulation is important to resting fishers in cold (and potentially hot) weather; thus, denser canopies may be correlated with physiological optima for fishers. Data on foot-loading in *Martes* species indicate that traveling in deep, soft snow is energetically demanding for fishers (Krohn et al. 2004). Thus, interception of snow by the forest canopy probably creates more favorable traveling and foraging conditions for fishers. Canopy cover may also be linked to other habitat conditions important to fishers but not measured directly, such as abundant prey and the presence of trees that provide many of the critical habitat features on which fishers depend for reproduction and resting.

It is clear that canopy cover is an important component of fisher habitat in western North America, and that results from previous studies of habitat ecology will continue to be widely used by resource managers. However, because investigators used different field and analytical methods to estimate canopy cover (Table 10.2), we were not able to make direct comparisons among studies or evaluate critical thresholds of canopy cover for fishers at different spatial scales. Thus, we encourage investigators to carefully consider issues of both terminology and measurement for canopy cover when presenting their findings and designing new studies. The term *canopy cover* is commonly used to describe various vegetation measures, regardless of the angle of

Table 10.2. Selected examples of different analytical and field methods used by investigators to estimate the amount of forest canopy associated with fisher distribution or occurrence (first-order habitat use or selection), fisher home ranges (second-order), or sites used by fishers (third-order) in western North America

Source	Attribute ^a	Method
First-order		
Carroll et al. 2001	Canopy cover	GIS data derived from classified satellite imagery ^b (30-m resolution), moving-average within a 30-km ² window
Davis et al. 2007	Canopy cover	GIS data derived from classified satellite imagery ^b (1-ha resolution), values calculated within a 10-km ² sample unit
	Canopy closure	Ground estimates of canopy closure based on visual assessments
Zielinski et al. 2010	Canopy cover	GIS data derived from classified satellite imagery ^b (1-ha resolution), values calculated within a 5-km ² moving window
Second-order		
Thompson et al. 2011	Canopy cover	GIS data derived from a combination of aerial photo interpretation and stand exam data
Weir and Corbould 2010	Canopy cover	GIS data derived from map-based ecosystem data
Zielinski et al. 2004a	Canopy cover	GIS data derived from a combination of several classified satellite images and aerial photography
Third-order		
Purcell et al. 2009	Canopy cover	Ground measurements using a moosehorn
Weir and Harestad 2003	Canopy cover	Ground estimates of vegetation cover based on visual assessments
Zielinski et al. 2004b	Canopy closure	Ground measurements using a densiometer

^a Canopy cover variables derived from GIS data were typically categorical, whereas canopy cover or closure variables derived from ground measurements (e.g., moosehorn, densiometer) were typically continuous

^b Methods used to classify satellite images, or to develop new aggregations of cover types from existing classified images, were different among first-order studies

view (Fiala et al. 2006). Specifically, however, canopy cover is the “proportion of the forest floor covered by the vertical projection of tree crowns,” whereas *canopy closure* is the “proportion of the sky hemisphere obscured by vegetation when viewed from a single point” (Jennings et al. 1999: 62). Using data from field plots on the Sierra Nevada National Forest, at which canopy measurements were collected using different methods (Landram 2002), Purcell et al. (2009) created regression equations for converting canopy estimates at fisher rest sites among 3 different measurement methods. Although the applicability of these regression equations to other forest types and regions has not been evaluated critically, Purcell et al. (2009) demonstrated that the estimates often varied in size by 20–30% between 2 commonly used ground methods to measure canopy cover (moosehorns) and closure (densiometers). Different ground methods used to estimate the same canopy attribute (e.g.,

canopy closure) also produced variable results (e.g., Fiala et al. 2006). Similarly, canopy-cover estimates derived from satellite imagery or other GIS data may not be directly comparable among studies because of differences in classification methods, resolution, and scaling of data (Table 10.2).

There is no ideal method for estimating canopy cover or closure; rather, the method should match the research objectives and the spatial scale of interest. For some objectives (e.g., identifying potential canopy-cover thresholds for fishers in the West), we recommend the development of a coordinated approach that can be used in all ecosystems where fishers occur that includes standardized methods for estimating canopy cover at different spatial scales. However, we also believe that additional insights about the importance of canopy to fishers are still needed, and we urge investigators to design studies that test specific hypotheses and identify other attributes to measure that are potentially linked to the amount of canopy, but may be of greater importance to fishers (e.g., microclimate, prey abundance).

Importance of Forest Composition and Age

Buskirk and Powell (1994) hypothesized that fishers in western North America may require old-growth conifer forests for survival, especially Douglas-fir forests. Habitat studies conducted during the past 2 decades, however, demonstrate that fishers are not dependent on old-growth forests, *per se*, nor do they appear to be associated with any particular forest type. Rather, fishers occur in a variety of low- and mid-elevation forest types and use a diversity of plant communities. Perhaps the most consistent attribute of fisher home ranges is that they comprise a mosaic of forest plant communities and seral stages, but often include relatively high proportions of mid- to late-seral forests. Thus, it is clear that habitat conditions other than those found in old-growth forests are capable of supporting fishers in western North America if adequate canopy cover, large structures for reproduction and resting, vertical and horizontal escape cover, and prey can be found.

Fisher distribution in the West has been associated consistently with low- to mid-elevation forests (e.g., Carroll et al. 2001; Zielinski et al. 2010; Spencer et al. 2011) and the proportion of the landscape that contains mid- to late-seral mixed-conifer or mixed conifer-hardwood forests (i.e., increasing amounts of medium and large-sized trees and complex structure; Carroll et al. 1999; Davis et al. 2007; Zielinski et al. 2010). Studies in eastern North America indicated that fishers are inefficient energetically when traveling and hunting in terrain covered by soft, deep snow (Raine 1983; Krohn et al. 2004). Thus, higher elevations in western North America that receive substantial snowfall appear to be less suitable for fisher occupancy because of increases in snowpack (Aubry and Houston 1992; Powell and Zielinski 1994; Krohn et al. 1997). We hypothesize, however, that other factors associated

ts (e.g., Fiala et al. 2006). Satellite imagery or other GIS data varies because of differences in type of data (Table 10.2).

canopy cover or closure; rather, variables and the spatial scale of interpotential canopy-cover thresholds development of a coordinated approach where fishers occur that includes canopy cover at different spatial scales. Insights about the importance of these variables led investigators to design studies to measure attributes that are not but may be of greater importance (Table 10.2).

Age

Fishers in western North America rely on forest for survival, especially Douglas-fir. In the past 2 decades, however, demand for old-growth forests, per se, nor do fishers select particular forest type. Rather, fishers select particular forest types and use a diversity of forest types as a consistent attribute of fisher home range. Forest plant communities and seral stages of mid- to late-seral forests, other than those found in older forests in western North America if reproduction and resting, vertical structure was found.

Associated consistently with low productivity (Zielinski et al. 2001; Zielinski et al. 2010; Spennemann et al. 2010) landscape that contains mid- to late-seral forests (i.e., increasing complexity and complex structure; Carroll et al. 2010). Studies in eastern North America found that fishers energetically when traveling and resting (Raine 1983; Krohn et al. 2004). In western North America that receive subsidies for fisher occupancy because of subsidies (Powell and Zielinski 1994; Zielinski et al. 1999), that other factors associated

with increasing elevation, including lower primary productivity and changes in forest structure (Franklin and Dyrness 1988; Meidinger and Pojar 1991), may also limit fisher distribution or abundance through their influence on the abundance of large structures needed for denning and resting and for providing an abundance of prey.

Fisher home ranges typically had moderate-to-high proportions of mid- and late-seral forests (on average, 42–72% of fisher home ranges; e.g., Zielinski et al. 2004a; Davis 2009), but we found no overarching patterns of selection for particular seral conditions or species composition at this scale (e.g., Higley and Matthews 2009; Weir and Corbould 2010). Results from analyses at other spatial scales were also variable (e.g., stands used within home ranges; Weir and Corbould 2008; Davis 2009; Higley and Matthews 2009); however, fishers rarely used the earliest seral conditions (e.g., herbaceous stage) or nonforested vegetation types (e.g., Weir and Harestad 2003; Aubry and Raley 2006; Purcell et al. 2009). We hypothesize that, when they establish their home ranges, it benefits fishers to include a diversity of available forest conditions, thereby increasing their access to a greater diversity and abundance of prey species while still providing habitat features important for reproduction and thermoregulation. The lack of any overarching patterns of selection by fishers for particular forest types or seral stages may also be due, in part, to differences in management history among locales and subsequent influences on forest structure. In northern California, young pole (10–29 year-old) and conifer-hardwood (≥ 30 year-old) stands selected for denning by reproductive females appeared to provide habitat similar to that typically found in older forests (≥ 80 years) because of the relatively high amounts of residual structure left in those stands when they were harvested (Higley and Matthews 2009). In the southern Sierra Nevada, forests have been altered substantially by almost a century of selective timber harvesting (McKelvey and Johnston 1992) and decades of fire suppression (Purcell et al. 2009). In portions of this region, fisher resting habitat is characterized by large legacy trees and snags surrounded by dense stands of smaller trees (Purcell et al. 2009).

Previously, it was thought that fishers in western North America may favor riparian forests (Buskirk and Powell 1994; Powell and Zielinski 1994); however, results from recent studies do not support this hypothesis. Although riparian forests were important to fishers in some locales (e.g., black cottonwood [*Populus balsamifera trichocarpa*] forests provided denning habitat in British Columbia; Weir and Corbould 2008), consistent use or selection for riparian forests has not been demonstrated. Several studies found that fisher rest sites were located closer to a stream or a body of water than random sites (e.g., Zielinski et al. 2004b; Yaeger 2005; Purcell et al. 2009). We caution against the assumption that all such results represent selection of riparian forests, however, because differences in vegetation composition between used

and random sites were not evaluated, and the width of riparian zones in mountainous terrain can be quite narrow (Brinson and Verhoeven 1999). Also, some studies used maps to identify the nearest stream to a fisher rest site, but they did not always determine the stream type (e.g., perennial, ephemeral) nor verify the presence of water at the time the sites were used by fishers (e.g., Seglund 1995; Purcell et al. 2009). Use of areas near water, in conjunction with other site conditions (e.g., low topographic position, steep slopes, high canopy cover), more likely reflects selection by fishers for cooler microclimates and, perhaps, for more productive sites (e.g., Zielinski et al. 2004b; Yaeger 2005; Purcell et al. 2009).

Several investigators have hypothesized that forests with a hardwood component, especially mast-producing species, may be more productive than others and provide fishers with diverse and abundant prey, and more den and rest structures (e.g., Carroll et al. 1999; Yaeger 2005; Purcell et al. 2009). Zielinski et al. (2004a) hypothesized that the greater abundance of forest types with black oak in the southern Sierra Nevada compared with coastal California enabled female fishers to occur at higher densities and meet their life needs within smaller home ranges. At finer spatial scales, some hardwood species clearly provide important structures for denning and resting (e.g., Reno et al. 2008; Weir and Corbould 2008; Higley and Matthews 2009). Selection by fishers for mixed conifer-hardwood forests has not been demonstrated, however, nor do we know whether such forests provide more resources for fishers. A better understanding of the importance of hardwood tree species for fishers, and of potential variation in their role in fisher habitat ecology among regions, represent important research needs.

Hierarchical Habitat Selection

Prior to 1994, few investigators incorporated spatial scale into their study designs explicitly. However, the overarching patterns we describe in this chapter indicate clearly that fishers use or select habitat in a hierarchical fashion. Hierarchical habitat selection is based on the premise that large-scale ecological processes occurring at relatively slow rates constrain those occurring at finer spatial scales at faster rates (e.g., Johnson 1980; King 1997). Hence, the fisher's geographic distribution (first-order selection) establishes the ecological niche that fishers can occupy successfully, which is further refined at the home range scale (second-order selection). The environments (third order) and resources (fourth order) selected by fishers within their home ranges are influenced and ultimately constrained by landscape-scale conditions and processes. Overall, environments and resources used or selected at all spatial scales by fishers are linked and collectively provide the annual and daily life needs of persistent populations.

the width of riparian zones in Brinson and Verhoeven 1999). The nearest stream to a fisher rest site was a stream type (e.g., perennial, intermittent) at the time the sites were used by fishers (e.g., Zielinski et al. 2009). Use of areas near water, in low topographic position, steep slopes, and selection by fishers for cooler temperatures were important factors in the selection of fisher habitat sites (e.g., Zielinski et al. 2009).

At forest scales with a hardwood component, hardwood forests may be more productive than other forest types, and more den and rest sites were found in hardwood forests (e.g., Purcell et al. 2009). Zielinski et al. (2009) found that abundance of forest types with a hardwood component compared with coastal California forests was related to the life needs of fishers. At landscape scales, some hardwood species may be more important for denning and resting (e.g., Reno et al. 2009; Matthews 2009). Selection by fishers for hardwood has not been demonstrated, however, and more resources for fishers are needed to understand hardwood tree species for fisher habitat ecology among

different spatial scales into their study. The patterns we describe in this chapter are habitat in a hierarchical fashion. The premise is that large-scale ecological processes constrain those occurring at smaller scales (e.g., King 1997). Hence, the selection of habitat at the landscape scale establishes the ecological context, which is further refined at the forest scale. The environments (third order) within their home ranges are shaped by landscape-scale conditions and processes, which are used or selected at all spatial scales to provide the annual and daily life

First-order habitat selection by fishers has been researched extensively in California (e.g., Carroll et al. 1999; Davis et al. 2007; Spencer et al. 2011), and to a lesser extent in the Rocky Mountains (Carroll et al. 2001). These studies have provided important insights about the landscape conditions that currently support fisher populations. Fisher occurrence was associated consistently with expanses of dense, structurally complex, and productive forests (based on tree biomass, greenness, wetness, and other indices of primary productivity). Landscape-scale abiotic factors, such as annual precipitation, topographic relief (i.e., landscape ruggedness), and elevation were also important in predicting fisher occurrence. The distribution of fishers was correlated with mid-elevation areas (Carroll et al. 2001; Zielinski et al. 2010) that had moderate levels of annual precipitation (Davis et al. 2007; Spencer et al. 2011), supporting the hypothesis that deep, persistent snow may limit fisher distribution (e.g., Krohn et al. 1997). Metrics of landscape ruggedness may actually represent forests with limited anthropogenic alterations, rather than the particular physiographic conditions that are selected by fishers. Although rigorous studies of first-order habitat selection have been conducted only in California, descriptive information from studies conducted elsewhere in western North America support the conclusion that fishers occur in a variety of low- to mid-elevation forests with relatively dense canopies (see Lofroth et al. 2010).

Within their distributional niche, fishers established home ranges comprising a mosaic of available forest types and seral stages, but contained relatively high proportions of mid- to late-seral forest conditions, moderate-to-dense canopy cover, and few open areas (e.g., Zielinski et al. 2004a; Higley and Matthews 2009; Weir and Corbould 2010). Our review did not reveal particularly strong selection at this scale, but that may reflect the limited number of studies that have been conducted at this scale (Table 10.1). Also, other factors that may influence the establishment of home ranges by fishers (e.g., landscape fragmentation, heterogeneity, edge ecotones) have not been well studied (but see Thompson et al. 2011).

Habitat use or selection by fishers was strongest and most consistent at finer spatial scales (third- and fourth-order selection). Fishers were associated with complex vertical and horizontal structure (e.g., large live trees, snags, and logs, and moderate-to-dense canopy cover), and they used or selected large structures characteristic of late-seral forests for reproduction and resting. What appeared most important to fishers at finer spatial scales were the ecological processes that create large structures with suitable microstructures for reproduction (cavities) and resting (e.g., cavities, mistletoe and rust brooms), and complex forest structure that provides security cover, favorable microclimates for thermoregulation, and, potentially, abundant prey.

Information Needed to Improve Management and Conservation

Research findings produced during the last 2 decades have now provided a foundational understanding of fisher habitat ecology in western North America, but we have identified various information needs throughout our review, as appropriate. Here, we present other significant information gaps that, if addressed adequately, would advance our understanding of the habitat-related factors that may influence fisher abundance and distribution and, ultimately, improve management and conservation efforts. Although our focus is habitat, we recognize that other factors not covered in this chapter, such as predation, competition, disease (Gabriel et al., this volume), and anthropogenic impacts (e.g., vehicle-related fisher mortalities), may also influence or limit the distribution and abundance of fishers.

Currently, there is limited information on the factors that may influence the selection of home ranges by fishers (second-order selection). Understanding whether home range establishment is mediated by forest type, canopy cover, abundance of structures, or prey (or a combination of factors) will be essential for maintaining or expanding fisher populations in western North America. This information is also needed to gain a better understanding of the amount and spatial configuration of forest conditions that fishers may need to meet their life needs, and the potential thresholds at which forest fragmentation (natural and anthropogenic) may preclude home range establishment and, thus, landscape occupancy.

Because fishers depend on structural elements to meet their reproductive and thermoregulatory needs, their habitat does not necessarily parallel that of their primary prey, as suggested by Buskirk and Powell (1994). Our understanding of fisher food habits has improved considerably; we know that the fisher's diet is diverse, varies regionally (Zielinski et al. 1999; Weir et al. 2005; Aubry and Raley 2006; Golightly et al. 2006), and is not as strongly linked to snowshoe hares as was suggested previously (Buskirk and Powell 1994). However, fisher foraging habitat remains undescribed and, although differences in prey diversity, abundance, and catchability among forest conditions may influence home range establishment by fishers (second-order selection) and habitat use at finer spatial scales (third- and fourth-order selection), no studies have tested these hypotheses.

Recent studies provide some evidence that female fishers are more selective than males for forest types at the home range scale (second order; Zielinski et al. 2004a) and for resting habitat at finer spatial scales (third and fourth order; Zielinski et al. 2004b; Yaeger 2005; Aubry and Raley 2006). Because fishers have a low reproductive capacity, and males do not contribute to the raising of young (Lofroth et al. 2010), the habitat needs of females are critical for population growth. More-focused investigations, or meta-analyses of

existing data, are needed to determine whether these apparent patterns of gender-based selection are consistent throughout western North America.

Few studies have investigated the abundance or spatial distribution of potentially limiting resources for fishers (Aubry and Raley 2006; Calabrese and Davis 2010). Given strong third- and fourth-order habitat use and selection by fishers (e.g., females are obligate users of tree cavities for reproduction), we recommend developing a common research approach for determining whether reproductive den structures are a limiting resource. Such an effort should be based on a sampling design that is applicable in all ecosystems where fishers occur in western North America, and focused on quantitative comparisons of the availability and spatial distribution of suitable structures (especially large live trees and snags with cavities) within female home ranges to correlates of fitness, such as reproductive success or kit recruitment. A similar approach could be used to test hypotheses regarding the potential scarcity of other resources (e.g., rest structures).

Finally, none of the studies we reviewed related correlates of fitness (e.g., reproduction, survival) to different forest conditions used or selected by fishers. Buskirk and Powell (1994) recognized the difficulty of collecting such measurements, but cautioned against the implicit assumption that resource selection confers greater fitness to individuals making those choices or that environments being selected are of higher quality than others. We believe that continuing advances in monitoring and analytical methods (e.g., radiotelemetry, noninvasive survey methods, occupancy analysis, and genetic and stable-isotope analyses; see Long and MacKay, this volume; Schwartz et al., this volume; Shirk et al., this volume; Slauson et al., this volume; C.M. Thompson et al., this volume) offer important new opportunities to researchers for relating fitness to habitat use or selection at multiple spatial scales and, ultimately, for quantifying fisher habitat quality in ways that will enable the development of more-comprehensive predictive models.

The overarching patterns of fisher habitat use or selection we have described in this chapter demonstrate strong support for some of the hypotheses proposed by Buskirk and Powell (1994; e.g., physical structure of stands is important, fishers avoid open environments) but limited support for others (e.g., importance of riparian forests). We found no support for their speculations that fishers in western North America depend on old-growth conifer forests or are primarily associated with Douglas-fir forests, or that the thermoregulatory needs of fishers do not influence habitat selection. However, many of the suggestions put forth by Buskirk and Powell (1994) to fill important knowledge gaps have not been implemented (e.g., investigate the effects of habitat fragmentation, relate prey catchability to forest structure and prey abundance, compare the structural conditions and prey associations selected by fishers in mixed broad-leaved forests in the East with those in mixed-conifer forests in the West). Thus, we encourage fisher researchers to design

2 decades have now provided a ecology in western North Amer- on needs throughout our review, ificant information gaps that, if lderstanding of the habitat-related and distribution and, ultimately, ts. Although our focus is habitat, n this chapter, such as predation, me), and anthropogenic impacts also influence or limit the distri-

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new kinds of studies that will effectively address these remaining knowledge gaps. Additionally, during the past 2 decades, an unprecedented number of high-quality datasets have been collected on fisher habitat ecology in western North America. These datasets provide potentially important opportunities for conducting quantitative meta-analyses (e.g., Buskirk et al. 2010) that would further elucidate the overarching patterns of habitat selection by fishers in western North America that we have described in this chapter.

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HASHAR