April 19, 2023

Public Comments Processing
Attn: FWS-R8-ES-2022-0166,
U.S. Fish and Wildlife Service, MS: PRB/3W
5275 Leesburg Pike,
Falls Church, VA 22041-3803

Introduction

The California Forestry Association (Calforests), American Forest Resource Council, National Alliance of Forest Owners, Pit and Fall River Resource Conservation Districts, the California Farm Bureau, The California Licensed Foresters Association, and the California Chapter of the Association of Consulting Foresters write to provide comments on the proposed rule, published by the U.S. Fish and Wildlife Service (Service), concerning the Endangered and Threatened Wildlife and Plants; California Spotted Owl: Endangered Status for the Coastal-Southern California Distinct Population Segment and Threatened Status with Section 4(d) Rule for the Sierra Nevada Distinct Population Segment. 88 Fed. Reg. 11,600 (Feb. 23, 2023).

Calforests is the preeminent trade association and advocate for California's forest products sector. Collectively, our members – private forestland owners – manage nearly 3.5 million acres of forestland throughout the State and operate nearly all of the state's forest products infrastructure, including sawmills, veneer mills, and biomass power plants. Our members are committed to working with the State to achieve our shared wildfire prevention and forest resiliency goals and we remain committed to working towards finding solutions that achieve a desirable outcome for all involved.

Notably, our member companies own and manage some 1.6 million acres of forestland within the range of the California Spotted Owl (CSO) Sierra Nevada population.

Like all forestland owners in California, they must undergo lengthy and expensive reviews of their Timber Harvest Plans to conduct forest management activities under what are the most restrictive timber harvesting laws in the United States. They have for years worked cooperatively with Service and responsible California agencies to avoid take of spotted owls (both Northern Spotted Owl (NSO) and CSO)). Some have Habitat Conservation Plans that cover not only NSO, but also CSO, and provide for the conservation of the species. These companies have invested decades and untold resources into science programs for spotted owls, monitoring the impacts of timber management practices on those species. They also have responded to the more recent challenges presented by wildfire to those species and their habitats in myriad ways, including by devoting more land and resources to fuelbreaks and other management prescriptions to reduce the risks posed by wildfire in state, public and private partnerships. These forestland owners remain committed to the conservation of spotted owls.

The American Forest Resource Council (AFRC) is a regional trade association whose purpose is to advocate for sustained-yield timber harvests on public forestlands throughout the West to enhance forest health and resistance to fire, insects, and disease. AFRC promotes active management to attain productive public forests, protect the value and integrity of adjoining private forests, and assure community stability. AFRC works to improve federal and state laws, regulations, policies, and decisions regarding access to and management of public forest lands and protection of all forest lands. AFRC represents over 50 forest product businesses and forest landowners throughout California, Idaho, Montana, Oregon, and Washington. These businesses provide tens of thousands of family-wage jobs in rural communities.

AFRC members depend on healthy and productive public forestland within the range of the CSO on the Lassen, Plumas, Tahoe, Eldorado, Stanislaus, Sierra, Sequoia, and Humboldt-Toiyabe National Forests. Forest health is also integral to reducing the likelihood of catastrophic wildfire that would further diminish the ability for those forests to maintain a robust and dependable timber program. The timber outputs on these National Forests contribute a critical component of the raw material necessary to keep our members' mills operating at full capacity. AFRC members Collins Pine, Franklin Logging, Trinity River Lumber, Sierra Forest Products, and Sierra Pacific Industries routinely procure forest products from the National Forests in the range of the CSO. The listing of the CSO could negatively impact the extent of vegetation management on National Forests within its range and the associated timber outputs and AFRC members' ability to procure those outputs to support their facilities. Unnecessary restrictions on such vegetation management would also frustrate efforts to reduce the risk of catastrophic wildfire.

The National Alliance of Forest Owners (NAFO) is a national advocacy organization committed to advancing federal policies that ensure our working forests provide clean air, clean water, wildlife habitat, and jobs through sustainable practices and strong markets. NAFO member companies own and manage more than 46 million acres of private working forests – forests that are managed to provide a steady supply of timber. NAFO's membership also includes state and national associations representing tens of millions of additional acres.

The Rural County Representatives of California (RCRC) is an association of forty rural California counties, and the RCRC Board of Directors is comprised of elected supervisors from each of those member counties. RCRC member counties contain much of California's forested lands, including more than 80 percent of the state's 20 million acres of national forest system lands. California county governments have also taken on increasing responsibilities to work with nonprofits, tribes and state and federal land managers to increase pace and scale of fuels treatment projects in and around communities in the wildland-urban interface in order to safeguard residents from the impacts of catastrophic wildfires, improve the quality and quantity of the state's water supply and provide a healthy ecosystem for California's wildlife.

The Pit and Fall River Resource Conservation Districts provide technical and financial assistance to agricultural producers and promote vegetation management to benefit stream channel stability and wildlife enhancement. Our missions are to protect, conserve, restore, and enhance natural resources for sustainability and economic diversity.

California Farm Bureau is California's largest farm organization, comprised of 53 county Farm Bureaus currently representing approximately 28,000 agricultural, associate, and collegiate members. Farm Bureau strives to protect and improve the ability of farmers, ranchers, and foresters engaged in production agriculture to provide a reliable, safe, and affordable supply of food and fiber through responsible stewardship of our natural resources.

The California Licensed Foresters Association (CLFA) was formed in 1980 and is committed to enhancing the role of professional forestry in California. CLFA represents all sectors of forestry including industrial, consulting, academic, state, and federal. It is the goal of the association to provide opportunities for continuing education and public outreach to its membership to further the forestry profession and responsible stewardship of California's forest lands.

The California Chapter of the Association of Consulting Foresters (ACF) are independent professionals who manage forests and market forest products for private woodland owners, called upon by landowners across the state and country to advance their forestland ownership goals.

The proposed rule divides the CSO population into two distinct population segments (DPSs) – a Sierra Nevada population and a Coastal-Southern California population. We believe there are serious questions and outstanding uncertainties as to whether dividing the CSO population into two distinct population segments is scientifically appropriate and lawful. We also question whether the Sierra Nevada population should be listed at all. Putting those concerns to the side, we wholeheartedly concur with the Service's finding that fire has had devastating impacts on the species. This letter focuses on the proposed Endangered Species Act section 4(d) rule for the Sierra Nevada population, and particularly the scope of its exception to the take prohibition for "[f]orest or fuels management to reduce the risk or severity of wildfire." 88 Fed.Reg. at 11,638-39.

This letter addresses the proposed 4(d) rule in two parts. First, the letter sets forth scientific information that demonstrates a broad range of forest management practices produce favorable CSO demographics. The Service considered some of the information, but not all best available science, and in certain instances did not properly interpret the data or give it the weight it deserves. Second, this letter explains, based on the relationship between forest management and favorable CSO demographics demonstrated by the data, why a 4(d) Rule should encompass a much broader range of forest management activities than what the Service appears to have proposed.

The Best Available Science Shows that Forest Management Is Necessary for CSO Recovery

Recent studies by leading CSO scientists show that, despite loss of individuals and habitat from fires, CSO populations on actively managed forestlands are stable or increasing in number. This is in stark contrast to the status of the owls on unmanaged forestlands, with studies showing the owl population on U.S. Forest Service (USFS) lands declining. Among leading CSO scientists, the data has driven the emergence of a consensus that managed forestlands are beneficial for the CSO relative to unmanaged forestlands. Moreover, the data indicates that managed forestlands not only reduce the risk of catastrophic wildfire – the primary threat to the CSO – but also promote the species' preferred prey, the dusky-footed woodrat, while continuing to provide adequate nesting and roosting habitat. These studies are summarized in Attachment A to this letter.

This represents a paradigm shift in CSO science. For decades, the prevailing view was that the species required late seral conditions for all of its habitats, and that owl activity centers had to be extremely large and not harvested to provide adequate nesting and roosting habitat for the species. This view often pitted effective forestland management against spotted owl conservation. But recent studies show this to have been a false choice. The new consensus comes none too soon, as the risks of catastrophic wildfire continue to increase with the march of climate change. Effective forest management is the only way to reduce that risk and provide for long-term sustainable recovered populations of CSO.

To summarize, the recent studies show:

- CSO are found on private forestlands at higher densities with higher occupancy and reproductive rates than on USFS lands (where CSO populations are actually decreasing).
- These higher occupancy and reproductive rates exist on heterogeneous landscapes containing various seral stages, as long as sufficient nesting and roosting habitats are available.
- Large high-intensity wildfires are detrimental to the species, while small low- to moderate-intensity wildfires are beneficial to or have no effect on the species.
- Forest management can help create a mosaic of burn severities allowing CSO to persist after a wildfire (in fact, forest management can create this desired heterogeneity even without fire).
- Forest management (including prescribed fires) promotes the CSO's preferred prey, thereby increasing the density, occupancy, and reproductive rates of the species.
- Intensive forest management across the landscape coupled with appropriate protection measures for known CSO sites promotes a stable to increasing population of the species.

Critically, the studies demonstrate that the beneficial effects of forest management for the CSO are produced by the full range of management actions and prescriptions, so long as adequate nesting and roosting habitat is available. Indeed, based on the studies it is questionable whether recovery can be expected even if the primary threat to CSO posed by wildfire can be effectively addressed by fuel breaks and conventional fuel treatments alone. While these efforts are necessary and hopefully can ameliorate the fire threat, the CSO needs additional management of the forests to provide the type and quantity of prey-producing habitat it needs to thrive.

In the Proposed Rule the Service considered some of these recent studies, but not all of them, and also failed to consider earlier studies containing information relevant to forest management and CSO demographics. We provide the studies the Service failed to consider with this letter and address their implications for forest management to conserve and recover the CSO. We also address those instances where the Service considered a study, but failed to properly interpret it or give it the weight it deserves.

Studies Not Considered by the Service

The table below identifies the studies the Service failed to consider and their key findings and implications for forest management and CSO demographics.[1]

Study	Key Findings and Implications
Hobart, B.K., et al. 2019b. Trophic interactions mediate response of predator populations to habitat change. Biological Conservation, 238 (108217).[2]	**Key Findings:** "At the local scale, spotted owl home range size significantly decreased as individual consumption of woodrats and pocket gophers increased." (pg 4) "We found a novel relationship between spotted owl occupancy dynamics and prey use: territory extinction probability was lower when owls consumed more woodrats and pocket gophers, indicating that owls were less likely to die at or abandon territories where such prey was readily consumed, presumably owing to energetic benefits." (pg 5) "In contrast to national forests, a greater reliance on woodrats and pocket gophers by spotted owls in national parks and private lands may contribute to relatively high owl abundance and occupancy rates in such landscapes." (pg 6) "Our results collectively suggest that restoration and management activities that promote key prey species may also benefit predator conservation, even if prey habitat does not necessarily reflect predator habitat (e.g., nesting areas)." (pg 6) **Implications:** The Discussion Section of this paper clearly highlights the importance of this research to management of forests to benefit the CSO: "On private lands, even-aged forest management may promote patches of young forest woodrat habitat (Sakai and Noon, 1993), particularly when landowners manage for the retention and recruitment of hardwood species (e.g., California black oak) and shrub cover (Innes et al., 2007; Gray et al., 2019). Although private lands have long been

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[1] All of the studies not considered by the Service in the Proposed Rule were also not considered in the Services' Species Status Assessment.

[2] This study is submitted with this letter as Attachment B.

	thought to provide only modest suitable habitat for spotted owls owing to active logging operations (Bias and Gutiérrez, 1992), such land management may benefit owls by providing key prey resources if younger forests with shrubs and hardwoods are juxtaposed with ample nesting and roosting habitat (older forest).” (pg 6) “Thus, although some uncertainties remain, our results provided a plausible mechanism to explain landscape-scale variability in spotted owl population measures and suggest that incorporating information about trophic interactions is an important prerequisite to understanding how predators respond to habitat differences among landscapes with contrasting land use histories and strategies.” (pg 6) “Specifically, promoting patches of brushy woodrat habitat and grassy pocket gopher habitat adjacent to closed canopy forests could enhance foraging opportunities for spotted owls. Our results also point to linkages among forest management, restoration, and species conservation: the regeneration of hardwoods – which has slowed owing to fire suppression – following natural and anthropogenic disturbance may simultaneously benefit woodrats, spotted owls, and forest restoration.” (pg 6) As can be seen from these results and conclusions for the first time in spotted owl science we have a very well-defined relationship between forest management and spotted owl demographics. To lessen the primary threat and provide prey for recovery of the CSO, almost all forest management moves towards those desired outcomes.
Kuntze, C.C., J.N. Pauli, C.J. Zulla,J.J. Keane, B.P. Dotters, K.N. Roberts, S.C. Sawyer, M.Z. Peery. Landscape heterogeneity provides co-benefits to predator and prey. 2023. In Review[3]	**Key Findings:** “Woodrat abundance was approximately 2.5x higher in owl home ranges featuring greater heterogeneity in vegetation types of mature forest, young forest, and open areas (1805.0 ± 50.2 SE) compared to home ranges dominated by mature forest (727.3 ± 51.9 SE), in large part

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[3] This study is submitted with this letter (it was not available at the time of publication of the proposed rule) as Attachment C.

	because of high densities in young forests that appeared to act as sources promoting woodrat densities in nearby mature forests." (pg 2) "A mosaic of vegetation types including young forest patches increased the abundance and availability of woodrats that, in turn, provided energetic and potentially reproductive benefits to mature forest-associated spotted owls." (pg 3) **Implications:** This research builds on the isotope paper by Hobart (2019b) above and confirms that active management produces the vegetation mosaics/heterogeneity that results in greater availability of the right prey species which leads to better occupancy and reproduction and thus to recovery. The same management reduces the potential for large-scale high intensity fires.
Zulla, C.J., Jones, G.M., Kramer, H.A., Keane, J.J., Roberts, K.N., Dotters, B.P., Sawyer, S.C., Whitmore, S.A., Berigan, W.J., Kelly, K.G., Gutiérrez, R.J., and Peery, M.Z. 2022b. In Review: Forest heterogeneity outweighs movement costs by enhancing hunting success and fitness in spotted owls.[4]	**Key Findings:** "…the benefits of mature forest on reproductive output were only realized when territories also had a high proportion of open forest." (pg 16) **Implications:** This paper may contain the most important finding related to recovery of the CSO. The very forest management that was considered detrimental to the CSO (based upon old research and perceptions) may present the answer to starting towards recovery of the CSO now that we have a better understanding based upon many dedicated researchers and these peer-reviewed results.

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[4] This paper was provided to the Service in an earlier review version, but the Service failed to consider it. This paper is submitted with this letter as Attachment D.

The Service's Misinterpretations of the Studies It Did Consider

The table below identifies the studies the Service appears to have considered but misinterpreted or given insufficient weight, and the implications of those studies for forest management and CSO demographics.

Study	Misinterpretation and Implication
Hobart, B.K., et al. 2021. Stable isotopes reveal unexpected relationships between fire history and diet of Spotted Owls. Ibis 163: 253-259.	**Misinterpretation:** The Service missed one of the major findings of the paper: "Here, we found that within national parks with long-standing (40+ years) fire management programmes, California Spotted Owls Strix occidentalis occidentalis consumed predominantly Woodrats Neotoma spp. and Pocket Gophers Thomomys spp.; however, in contrast to our predictions, when their territories experienced more extensive and frequent fire, Spotted Owls consumed proportionally more Flying Squirrels Glaucomys oregonensis." (pg 1) **Implication:** This paper helps confirm that both forest management generally and active prescribed fire management can produce beneficial prey, but that catastrophic large-scale fires lead to greater consumption of less-nutritious prey, possibly resulting in known long-term demographic declines on USFS lands due to a lack of both forest management and prescribed fire.
[SPI] Sierra Pacific Industries, Roberts KN, Dotters BP, et al. 2022. Occupancy, Status and Movement of the California Spotted Owl associated with Forest Management Activities in the Sierra Nevada of California 2012 through 2021	**Misinterpretation:** The Service missed one of the major conclusions of the paper: "Movement, occupancy and social status of known CSO sites do not appear to be affected by these timber harvest units in the years following the harvest. Movement of the AC occur every year at nearly all sites for various reasons, timber harvest does not appear to affect the distance moved." (pg 17) **Implication:** The important conclusion here is that because intensive forest management on managed industrial forestland did not have a measurable impact on CSO movement, occupancy, or status, forest management generally should be conducted to reduce fire risk and provide favorable habitat for CSO,

	and should not be limited to less intensive management of fuel breaks and fuel reductions.
Atuo, F.A., K. Roberts, S. Whitmore, B.P. Dotters, M.G. Raphael, S.C. Sawyer, J.J Keane, R.J. Gutierrez, and M.Z. Peery. 2019. Resource selection by GPS-tagged California spotted owls in mixed ownership forests. Forest Ecology and Management 433, pp 295-304**.**	**Misinterpretation:** The Service chose to emphasize a statement concerning hourly vs. nightly foraging patterns: "owls selected for intermediate- and large-sized trees with high canopy cover." (pg 302) The Service did not cite the key finding that spotted owls use all habitats in proportion to their availability (as demonstrated by their overlapping confidence intervals). (pg 301 and Figure 6) **Implication:** This research on 53 GPS tagged owls during the fledging support season, being the largest number of owls ever included in a single study, helps to demonstrate that CSO are indeed forest generalists and use all forest types as they are available.
Kramer, H.A., G.M. Jones, S.A. Whitmore, J.J. Keane, F.A. Atuo, B.P. Dotters, S.C. Sawyer, S.L. Stock, R.J. Gutiérrez, and M.Z. Peery. 2019. California spotted owl habitat selection in a fire-managed landscape suggests conservation benefit of restoring historical fire regimes. Forest Ecology and Management, 479, p.118576.	**Misinterpretation:** The Service cited this study only once (in the Federal Register at 11,605) and that was to cherry pick one foraging conclusion while avoiding the rest of the key findings of the paper which was focused on restoring historical fire regimes and resulting conservation benefits to the CSO. **Implication:** This paper supports doing all we can to arrest the trend towards large-scale high-intensity fires and return to historic mosaic pattern fires or mimic such outcomes by active management without fire.
Zulla, C.J., H.A. Kramer, G.M. Jones, J.J. Keane, K.N. Roberts, B.P. Dotters, S.C. Sawyer, S.A. Whitmore, W.J. Berigan, K.G. Kelly, A.K. Wray, and M.Z. Peery. 2022. Large trees and forest heterogeneity facilitate prey capture by California Spotted Owls. Ornithological Applications 124:duac024.	**Misinterpretation:** The Service cited (in the Federal Register at 11,609): "Odds ratios indicated that with each 10% increase in medium trees/medium canopy cover forest, the odds of prey capture increased by a factor of 1.20 (i.e. a 20% increase in odds)." (pg 8) The Service missed one of the major findings of the paper: "Spotted Owls tended to capture woodrats in areas with more young forest, more medium trees/medium canopy cover forest, more large trees/medium canopy cover forest, more large trees/high canopy cover

	forest, in areas with a higher density of hardwood edges, and areas with higher forest heterogeneity. Odds ratios indicated that the odds of prey capture increased by a factor of 1.39 with every 10% increase in young forest and by a factor of 1.33 with every 10% increase in medium trees/medium canopy cover forest. The odds of prey capture increased by a factor of 1.60 with every 10% increase in large trees/medium canopy cover forest and 1.61 with every 10% increase in large trees/high canopy cover forest. Each 10 m ha–1 increase in hardwood edge increased the odds of prey capture by a factor of 1.73, and each 10% increase in cover type heterogeneity increased the odds of prey capture by a factor of 1.22." (pg 8) **Implication:** This paper builds on the stable isotope paper (Hobart 2019b) and continues to support the conclusion that forest management and prescribed fire both produce beneficial heterogeneity for the preferred prey species and lead to recovery.

The studies set forth in the above tables carry forward and confirm the insight contained in Franklin's seminal paper that increased fitness and demographic stability can be achieved when prey-producing habitat is intermixed with nesting habitat. Ecological Monographs, 70(4), pp. 539-590 (1999). This paper is summarized in Attachment A to this letter.

The Proposed 4(d) Rule Should Cover All Forest Management That Provides Adequate CSO Nesting and Roosting Habitat Because It Is Vital for Recovery

The evidence is clear that intensive forest management is essential to the conservation and recovery of the CSO. The proposed 4(d) Rule should be clarified so that it more clearly encompasses all forest management that provides adequate CSO nesting and roosting habitat. The "forest or fuels management" exception to the take prohibition in the proposed 4(d) Rule would cover:

> Forest or fuels management to reduce the risk or severity of wildfire (such as prescribed fire) where fuels management activities are essential to reduce the risk of catastrophic wildfire, and when such activities will be carried out in accordance with an established and recognized fuels or forest management plan that includes measures to minimize impacts to the California spotted owl and its habitat and results in conservation benefits to California spotted owls. 88 Fed.Reg. at 11,639.

For the avoidance of doubt, the Service should clarify that “forest management plan” includes the full panoply of timber operations authorized by a Timber Harvest Plan (or other plan) under the California Forest Practice Act and Forest Practice Rules. As explained above, such forest management, so long as it provides for adequate nesting and roosting habitat, is critical to the conservation and recovery of the CSO. More particularly, as long as active nests are seasonally protected (approximately 70 acres) and so long as adequate nesting and roosting habitat (roughly 50% of the landscape within 0.5 miles is 11” QMD and 50% canopy closure) is available post-harvest there should be no other constraints on forest management activities on private landowners in California. Additionally, outside of the breeding season, forest management can occur in these seasonally protected areas and benefit fuel reduction and prey production. These limited constraints are proposed because all timber operations are beneficial to reducing fuel loading and have beneficial impacts on fire behavior and prey production. Increased prey production and fire threat reduction will lead to the recovery of the CSO.

To this end, the Service should also reconsider its approach to historic activity centers, which results in long-unoccupied forest stands highly susceptible to wildfire because they have not been managed. These fuel-laden historic activity centers put occupied activity centers at risk, posing a serious threat to the CSO.

Our organizations and their members look forward to working with the Service to refine the proposed 4(d) rule so that it can more effectively protect the species from catastrophic wildfire and support the creation of favorable habitat conditions supporting the recovery of the species.

Thank you for your consideration.

Sincerely,

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Attachment A

Summary of Studies re California Spotted Owl Habitat Requirements

Below is an annotated bibliography summarizing spotted owl studies that were not considered or misinterpreted by the Service in reviewing the available science for its Proposed 4(d) Rule for the CSO. The studies are summarized in chronological order.

Franklin, A.B., D. R. Anderson, R.J. Gutierrez, and K.P. Burnham. 2000. Climate, Habitat Quality, and Fitness in Northern Spotted Owl Populations in Northwestern California. Ecological Monographs, 70(4), pp 539-590.

- Annual survival on territories was positively associated both with amounts of interior old-growth forest and with length of edge between those forests and other vegetation types.
- Reproductive output was negatively associated with interior forest, but positively associated with edge between mature and old-growth conifer forest and other vegetation types.

Jones, G.M., R.J. Gutierrez, D.J. Tempel, S.A. Whitmore, W.L. Berigan, and M.Z. Peery. 2016. Megafires: an emerging threat to old-forest species. Frontiers in Ecology and the Environment 14:300-306.

- The probability of owl site extirpation was seven times higher after the fire (0.88) than before the fire (0.12) at severely burned sites, contributing to the greatest annual population decline observed during our 23-year study.
- The fire also rendered large areas of forest unsuitable for owl foraging one-year post-fire.
- Megafires pose a threat to old-forest species, and we conclude that restoring historical fire regimes could benefit both old-forest species and the dry forest ecosystems they inhabit in this era of climate change.

Roberts, K., W.E. Hall, A.J. Shufelberger, M.A. Reno, and M.M. Schroeder. 2017. California spotted owl occupancy on mixed ownership lands in the Sierra Nevada of California, 2012 through 2016. Northwestern Naturalist 98:101-116.

- CSOs occurred on industrial timberlands.
- CSOs occur at higher densities and occupancy rates in a mixed ownership than on US Forest Service lands.

Atuo, F.A., K. Roberts, S. Whitmore, B.P. Dotters, M.G. Raphael, S.C. Sawyer, J.J Keane, R.J. Gutierrez, and M.Z. Peery. 2019. Resource selection by GPS-tagged California spotted owls in mixed ownership forests. Forest Ecology and Management 433, pp 295-304.

- Spotted owls selected areas with relatively high cover type heterogeneity that included a mix of seral stages, except in the core of their home range where they selected relatively spatially homogenous forests characterized by large trees and closed canopy.
- These results indicate that landscapes having forest patches characterized by either intermediate or large-sized trees, both with high canopy cover, likely constitute the important foraging habitat for CSOs in Sierra Nevada mixed conifer forests.
- All habitat types were used in proportion to the availability.

Hobart, B.K., K.N. Roberts, B.P. Dotters, W.J. Berigan, S.A. Whitmore, M.G. Raphael, J.J. Keane, R.J. Gutierrez and M.Z. Peery. 2019a. Site occupancy and reproductive dynamics of California spotted owls in a mixed-ownership landscape. Forest Ecology and Management. 437, pp 188-200.

- Site occupancy probability was higher at low-elevation sites and lower at sites that contained more open area and younger forest.
- Successful reproduction by owls was also more likely at low elevation sites and at sites with more north-facing slopes and younger forest with high basal area of hardwoods.
- Study areas with more private lands tended to occur at lower elevations and have greater amounts of younger forest with high basal area of hardwoods, which may have contributed to higher occupancy and reproductive probabilities than the study area with more public land.
- Differences in occupancy and reproductive probabilities between study areas appeared to be the result of differences in topographic and vegetation conditions that likely promote populations of key spotted owl prey species.
- Our results suggest that private lands in mixed-ownership landscapes may contribute to spotted owl conservation by conferring different benefits to owls than public lands.

Hobart, B.K., G.M. Jones, K.N. Roberts, B.P. Dotters, S.A. Whitmore, W.J. Berigan, M.G. Raphael, J.J. Keane, R.J. Gutierrez, M.Z. Peery. 2019b. Trophic interactions mediate response of predator populations to habitat change. Biological Conservation, 238(108217).

- Consumption of woodrats and pocket gophers, which varied with habitat conditions, was associated with smaller home ranges and lower territory extinction probabilities.
- Spotted owls consumed significantly more woodrats and pocket gophers in landscapes with stable (national parks) and high-occupancy (private lands) populations than in landscapes with declining owl populations (national forests).
- Managing for important prey species habitat may benefit predator populations.

Kramer, H.A., G.M. Jones, S.A. Whitmore, J.J. Keane, F.A. Atuo, B.P. Dotters, S.C. Sawyer, S.L. Stock, R.J. Gutiérrez, and M.Z. Peery. 2019. California spotted owl habitat selection in a fire-managed landscape suggests conservation benefit of restoring historical fire regimes. *Forest Ecology and Management*, *479*, p.118576.

- Our findings are consistent with the hypothesis that CSOs are adapted to historical frequent-fire regimes of overall lower-severity with small high-severity patches.
- We hypothesize that fire management, coupled with medium- and large-tree retention, likely maintains high quality spotted owl habitat and may contribute to the observed owl population stability in Sequoia and Kings Canyon National Parks, compared to declining populations on three national forests.
- Finally, our results indicated that fire management, as practiced in these national parks, could benefit owl conservation elsewhere if challenges to the reintroduction of frequent-fire regimes can be overcome

Jones, G.M., Kramer, H.A., Whitmore, S.A., Berigan, W.J., Tempel, D.J., Wood, C.M., Hobart, B.K., Erker, T., Atuo, F.A., Pietrunti, N.F. and Kelsey, R., 2020. Habitat selection by spotted owls after a megafire reflects their adaptation to historical frequent-fire regimes. Landscape Ecol; doi.org/10.1007/ s10980-020-01010-y.

- Our results support the hypothesis that spotted owls are adapted to historical fire regimes characterized by small severe fire patches in this region. Shifts in disturbance regimes that produce novel landscape patterns characterized by large, homogeneous patches of high-severity fire may negatively affect this species.

Jones, G.M., Kramer, H.A., Berigan, W.J., Whitmore, S.A., Gutiérrez, R.J. and Peery, M.Z., 2021. Megafire causes persistent loss of an old-forest species. *Animal Conservation*, *24*(6), pp.925-936.

- We found that extensive severe fire within spotted owl sites resulted in both immediate site abandonment and prolonged lack of re-colonization by owls six years post-fire.
- Our study demonstrates the prolonged effects of severe fire on the occupancy of this forest-dependent species, suggesting that forest restoration that reduces megafires could benefit spotted owls.

Jones, G.M., Keyser, A.R., Westerling, A.L., Baldwin, W.J., Keane, J.J., Sawyer, S.C., Clare, J.D., Gutiérrez, R.J. and Peery, M.Z., 2022. Forest restoration limits megafires and supports species conservation under climate change. Front. Ecol. Environ., doi:10.1002/fee2450.

- Our findings suggest restoring historical forest structure may mitigate severe fire activity as the climate warms, particularly when restoration occurs in owl habitat.
- Benefits provided by restoration to owls (reduced severe fire) were found to exceed potential costs (direct habitat alteration) by mid-century.

SPI. 2022a. California Spotted Owl Surveys and Monitoring on SPI Lands in the Sierra Nevada 2021 Annual Report and 2012-2021 Summary Report. Provided the California Department of Fish and Wildlife per SCP-11963.

- Continued stable to increasing population of California spotted owls on intensively managed private timberlands.

SPI. 2022b. Draft report. Occupancy, Status and Movement of the California Spotted Owl associated with Forest Management Activities in the Sierra Nevada of California. 2012 through 2021. Provide to USFWS per HCP, Permit #TE84089D-0.

- Given the findings of Hobart et al. (2019), Atuo et al (2018) and this in-depth analysis of harvesting effects on AC status and movement, sustainable timber harvesting coupled with appropriate protection measures, can be compatible with, and even help support, a sustaining population of CSOs.
- These CSO WSAs demonstrate a population of owls that have high and steady occupancy, high percentage of pairs and a higher density of owls comparatively to long standing US Forest Service study areas; all within a landscape with timber harvest.
- Movement, occupancy and social status of known CSO sites do not appear to be affected by these timber harvest units in the years following the harvest.
- Movement of the AC occurs every year at nearly all sites for various reasons with or without harvest; timber harvest does not appear to affect the distance moved.
- There was no effect or difference on occupancy for harvested or unharvested sites. This no effect result did not change over for the 5 years following harvesting.

Kuntze, C.C., J.N. Pauli, C.J. Zulla, J.J. Keane, B.P. Dotters, K.N. Roberts, S.C. Sawyer, M.Z. Peery. Landscape heterogeneity provides co-benefits to predator and prey. 2023. In Review

- A mosaic of vegetation types including young forest patches increased the abundance and availability of woodrats that, in turn, provided energetic and potentially reproductive benefits to mature forest-associated spotted owls.
- Strong empirical evidence that heterogeneous landscapes containing prey refuges can benefit both predator and prey populations.

Zulla, C.J., Kramer, H.A., Jones, G.M., Keane, J.J., Roberts, K.N., Dotters, B.P., Sawyer, S.C., Whitmore, S.A., Berigan, W.J., Kelly, K.G., Wray, A.K., Gutiérrez, R.J., and Peery, M.Z. 2022a *Large trees and forest heterogeneity facilitate prey capture by California Spotted Owls.* Ornithological Applications 124(3):1-14. https://doi.org/10.1093/ornithapp/duac024 .

- Our results suggest that promoting large trees, increasing forest heterogeneity, and creating canopy gaps in forests with medium trees/high canopy cover could benefit Spotted Owls and their prey, which has the ancillary benefit of enhancing forest resilience.

Zulla, C.J., Jones, G.M., Kramer, H.A., Keane, J.J., Roberts, K.N., Dotters, B.P., Sawyer, S.C., Whitmore, S.A., Berigan, W.J., Kelly, K.G., Gutiérrez, R.J., and Peery, M.Z. 2022b. *In Revision:* Forest heterogeneity outweighs movement costs by enhancing hunting success and fitness in spotted owls.

- Spotted owl reproductive output, unexpectedly, decreased with increasing proportional areas of mature forest, as well as decreased with more open forest.
- Reproductive output was relatively high when territories contained greater proportional areas of both mature and open forests.
- Enhanced prey access, hunting success, and deliveries to nests in territories with a mosaic of forest stand ages – and edges between forest stands – can lead to emergent benefits to spotted owl fitness in some ecological settings.
- The benefits of mature forest on reproductive output were only realized when territories also had a high proportion of open forest

Wilkinson, Z.A., H.A. Kramer, G.M. Jones, C.J. Zulla, K. McGinn, J.M. Barry, S.C. Sawyer, R. Tanner, R. J. Gutierrez, J.J. Keane, M.Z. Peery. 2023. Tall, heterogeneous forest improve prey capture, delivery to nestlings, and reproductive success for Spotted Owls in southern California. Ornithological Applications, duac048.

- Foraging owls were more successful capturing prey, including woodrats, in taller multilayered forests, in areas with higher heterogeneity in vegetation types, and near forest-chapparal edges.
- Spotted Owls delivered prey items more frequently to nests in territories with greater heterogeneity in vegetation types and delivered prey biomass at a higher rate in territories with more forest-chaparral edge.
- Spotted Owls had higher reproductive success in territories with higher mean canopy cover, taller trees, and more shrubby vegetation.
- our results provide additional and compelling evidence that a mosaic of large tree forest with complex canopy and shrubby vegetation increases access to prey with potential reproductive benefits to Spotted Owls in landscapes where woodrats are a primary prey item.
- We suggest that forest management activities that enhance forest structure and vegetation heterogeneity could help curb declining Spotted Owl populations while promoting resilient ecosystems in some regions.
- This study adds to the growing body of literature indicating that forest management activities intended to promote forest heterogeneity could benefit the conservation of the spotted owl.

Attachment B

Hobart, B.K., et al. 2019b.

Attached is a copy of Hobart, B.K., G.M. Jones, K.N. Roberts, B.P. Dotters, S.A. Whitmore, W.J. Berigan, M.G. Raphael, J.J. Keane, R.J. Gutierrez, M.Z. Peery. 2019b. Trophic interactions mediate response of predator populations to habitat change. Biological Conservation, 238(108217).[1]

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[1] This study is submitted with CFA et.al. comment letter on the proposed listing of the CSO as Attachment B.

Biological Conservation 238 (2019) 108217

Contents lists available at ScienceDirect

Biological Conservation

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

Trophic interactions mediate the response of predator populations to habitat change

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ARTICLE INFO

Keywords:
Ecological mechanisms
Foraging
Forest management
Predator conservation
Spotted owl
Stable isotope analysis

ABSTRACT

Identifying the mechanisms by which globally pervasive changes in habitat affect predators is a central, yet challenging, endeavor in applied ecology. Cryptic shifts in trophic interactions are potentially important but widely underappreciated mechanisms shaping predator population response to habitat change. Here, we assessed the extent to which variation in trophic interactions explained differences in predator populations at both local and landscape scales. We integrated stable isotope analyses, GPS tagging, and long-term territory occupancy information to characterize the trophic ecology of spotted owls in the Sierra Nevada, California, USA where population trends and densities vary among forest landscapes with contrasting land uses and disturbance regimes. Trophic interactions appeared to influence spotted owl space use and territory occupancy rates with emergent consequences for landscape-scale patterns in population abundance and trends. Specifically, consumption of woodrats and pocket gophers, which varied with habitat conditions, was associated with smaller home ranges and lower territory extinction probabilities. Moreover, spotted owls consumed significantly more woodrats and pocket gophers in landscapes with stable (national parks) and high-occupancy (private lands) populations than in landscapes with declining owl populations (national forests). Collectively, our results suggest that trophic responses to local habitat conditions can affect predators at multiple spatial scales and that managing for important prey species habitat may benefit predator populations. Because trophic interactions mediate species' responses to anthropogenic pressures in many ecological systems, our approach to integrating stable isotopes with behavioral, fitness, occupancy, and demographic data offers a tractable avenue for researchers elsewhere to quantify such relationships.

1. Introduction

As human-driven extinctions accelerate, understanding the factors that cause population declines is a central, yet challenging, goal in applied ecology (Ceballos et al., 2017). It is increasingly recognized that interspecific interactions play an important role in shaping the response of species to anthropogenic habitat loss and degradation (Stier et al., 2016). Trophic interactions (i.e., consumer-resource relationships) in particular may affect whether and to what degree habitat alterations lead to changes in population trends, given that resource consumption can influence key aspects of species' life histories (Elton, 1927). Indeed, resource use can modify individual space-use behavior (and thus energetic budgets; Schoener, 1968), fine-scale demographics (Moss et al., 2016b), and broad-scale patterns in abundance (Chamberlain et al., 2005). Thus, understanding the interplay among habitat changes, trophic interactions, and population trends may be an important prerequisite to reversing species declines, conserving biodiversity, and restoring functional relationships to ecosystems (Stier et al., 2016).

Predators are particularly prone to diet-mediated responses to habitat change because of their higher trophic position and dependence on spatially and temporally variable prey resources (Elton, 1927; Moss et al., 2016b). Because predator diets are often relatively plastic (Darimont et al., 2009), local shifts in habitat structure and abundance that alter resource availability may lead to concomitant changes in trophic interactions between predators and their prey. In some cases, trophic plasticity may allow predators to exploit novel resources in

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https://doi.org/10.1016/j.biocon.2019.108217
Received 18 May 2019; Received in revised form 9 August 2019; Accepted 22 August 2019

highly impacted ecosystems (Moss et al., 2016a). Yet, individuals may also incur fitness consequences when bottom-up shifts in resource availability result in reliance on low-quality resources (Heiss et al., 2009). Thus, for predators, local-scale variability in trophic interactions may cause both positive and negative responses to anthropogenic habitat changes.

Local, individual-level variation in trophic interactions may have emergent consequences for predator populations at broad spatial scales (Levin, 1992). In landscapes where predators consume high-quality (i.e., large-bodied and/or high-density) prey, elevated fitness can promote positive population growth (Benton et al., 2006) and smaller home ranges can increase population densities (McNab, 1963). However, because consumptive patterns are logistically challenging to quantify, they are seldom evaluated alongside habitat factors as drivers of predator population change over broad extents (Rosado et al., 2016). This constraint has contributed to the viewpoint suggested by some ecologists that interspecific interactions may be unnecessary to consider at coarse grains and large spatial scales (Soberón and Nakamura, 2009). Thus, despite the importance of predation to ecosystem processes (Estes et al., 2011), the role that trophic interactions play in mediating predator population response to anthropogenic habitat change is poorly understood.

Here, we assessed whether trophic interactions mediate the response of predator populations to anthropogenic habitat alteration, focusing on a territorial old-forest species, the California spotted owl *Strix occidentalis occidentalis* (hereafter "spotted owl"). In the Sierra Nevada, USA, spotted owl population status varies among forested landscapes that differ in structure owing to contrasting human land use practices on national parks, national forests, and private lands (e.g., Collins et al., 2017). Populations are declining on national forest-dominated landscapes, where selective logging and a century of fire suppression have created dense, homogeneous forests with a large-tree deficit (Jones et al., 2018). By contrast, populations appear stable or increasing on national parks, where timber harvest restrictions and the partial restoration of frequent-fire regimes have promoted more heterogeneous forests dominated by large trees (Collins et al., 2017). Finally, spotted owl territory occupancy is unexpectedly high in landscapes dominated by private lands managed for timber production that contain a mosaic of younger, even-aged forest stands (Hobart et al., 2019). Although patterns of spotted owl population status are well-described, the ecological mechanisms linking forest management and conditions to such patterns remain uncertain (Peery et al., 2017).

We hypothesized that trophic interactions mediate spotted owl population response to habitat differences among national forests, national parks, and private landscapes. Spotted owls consume a diverse array of small mammals and other taxa, but flying squirrels *Glaucomys oregonensis* and woodrats *Neotoma* spp. dominate their diet by biomass in our study region (Verner et al., 1992). Whereas flying squirrels are associated with mature, closed-canopy forests (Waters and Zabel, 1995), woodrats utilize a wider range of forest conditions. Dusky-footed *N. fuscipes* and big-eared woodrats *N. macrotis* are relatively abundant in younger forests with ample hardwoods at lower elevations (Innes et al., 2007) but bushy-tailed woodrats *N. cinerea* reside in both young and mature forests – often near rocky features – at higher elevations (Carey et al., 1999). All three woodrat species also occupy riparian forests and utilize cavities in old trees, snags, and downed debris (Innes et al., 2007). Given their habitat associations, it is possible that anthropogenic changes to forest structure (e.g., fire suppression, restoration, and timber extraction) have altered the distribution and abundance of flying squirrels and woodrats in the Sierra Nevada. Moreover, although both are important prey for spotted owls, woodrats are higher-density (up to 40 acre^{-1} versus ~1 acre^{-1}; Williams et al., 1992) and provide more energy per prey (1205 kJ versus 592 kJ; Weathers et al., 2001), and thus may be more energetically profitable prey when present (i.e., higher-quality). Thus, because prey availability may vary among landscapes and with owl population status in the Sierra Nevada, this system offers a valuable opportunity to investigate whether trophic interactions mediate population response to anthropogenic habitat change and, in the process, resolve a longstanding uncertainty for a model species in population and landscape ecology.

We integrated stable isotope analyses with individual movement, territory occupancy, and remotely-sensed vegetation data to test three predictions related to our central hypothesis. First, at the local (territory) scale, we predicted that the prevalence of hardwoods, degree of forest heterogeneity, and presence of young forest would promote consumption of woodrats by owls, whereas medium-aged and older forest would promote consumption of flying squirrels. Second, we predicted that consumption of woodrats by owls would be associated with (i) smaller home range sizes and (ii) lower territory extinction rates. Third, at the landscape scale we predicted that spotted owls would consume primarily woodrats on private lands, flying squirrels on national forests, and an intermediate mixture on national parks. Thus, we predicted that consumption of woodrats would roughly positively correspond with landscape-scale population status. By testing these predictions across landscapes with different management strategies and ecological conditions, we offer insights into the role of trophic interactions as mechanisms that shape the response of predator populations to anthropogenic habitat change.

2. Methods

2.1. Study system

We studied spotted owls across the Sierra Nevada bioregion, USA (Fig. 1) as part of ongoing research (e.g., Atuo et al., 2019; Hobart et al., 2019; Jones et al., 2018). We surveyed for spotted owls on all major landownerships in the region, including national parks (Yosemite and Sequoia-Kings Canyon), national forests (Lassen, Plumas, Tahoe, Eldorado, Stanislaus, and Sierra), and private lands (primarily land owned by Sierra Pacific Industries). Generally, private lands occurred at lower elevations, national forests at intermediate elevations, and national parks at higher elevations (Table S1). National parks also occurred, on average, at lower latitudes than both national forests and private lands (Table S1).

2.2. Field and laboratory methods

We captured 142 adult spotted owls using established methods (Franklin et al., 1996) early in the breeding seasons (April–July) of 2017 and 2018. At the time of capture, we sampled 1–2 growing or recently grown body feathers per owl for isotopic analysis. Because feather is an inert tissue that reflects the diet for the period it was synthesized (Hobson and Clark, 1992) and spotted owls molt body feathers during the breeding season (Forsman, 1981), our samples reflected the diet for the current breeding season. We affixed GPS transmitters to a subset of 49 owls to quantify home range sizes (see Atuo et al., 2019 for details). We also opportunistically collected regurgitated spotted owl pellets to obtain count-based diet estimates and process prey bones for isotopic analysis. All animal research was approved by the University of Wisconsin institutional animal care and use committee and permitted by the necessary state and federal agencies.

We rinsed feathers 3× with 2:1 chloroform:methanol to remove contaminants, homogenized them with scissors, and dried them at 55 °C for ≥72 h. We first soaked prey bones in 0.5 N HCl for ≥48 h to remove calcium and associated inorganic carbon. Second, because dietary proteins, but not lipids, are typically routed to feather keratin (Bearhop et al., 2002), and lipid-based carbon differs isotopically from protein-based carbon (Post et al., 2007), we soaked prey bones 3× in 2:1 chloroform:methanol for 24 h to extract lipids. Third, we dried bones at 55 °C for ≥72 h and crushed them with scissors. Feather and bone samples were weighed in tin capsules for δ^{13}C and δ^{15}N analysis at the University of New Mexico Center for Stable Isotopes on a Thermo

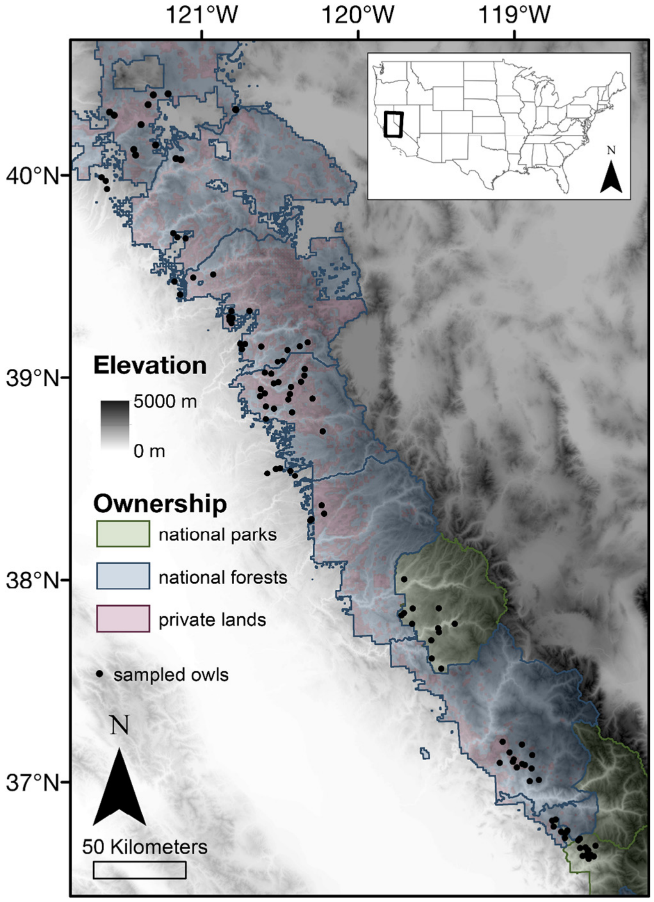

Fig. 1. Map of the Sierra Nevada, USA depicting locations where spotted owl feathers were sampled for isotopic analyses. Thick lines denote federal administrative boundaries and colored shading denotes ownership within such boundaries. Territories outside federal boundaries occurred on private lands.

Scientific Delta V mass spectrometer connected to a Costech 4010 elemental analyzer and a high-temperature conversion elemental analyzer. Results were expressed as parts per mil (‰) ratios relative to the international standards Vienna Peedee Belemnite (C) and atmospheric nitrogen (N).

2.3. *Quantifying owl territory characteristics*

We modeled owl diet as a function of habitat covariates (Table 1). We included elevation and latitude of owl territory centers because both variables are associated with prey species distributions. We included four forest age class covariates (open, young, medium, and old), as well as Shannon's diversity index (H) of such classes to estimate forest heterogeneity. We also included the mean basal area of hardwoods within owl territories. We calculated forest covariates using gradient-nearest-neighbor (GNN) maps (2012, lemma.forestry.oregonstate.edu) within 1270.5 ha circular buffers around owl territory centers (roosts and nests). Buffer size corresponded to the mean home range area (95% kernel density estimate [KDE]) of GPS-tagged owls calculated using the R package adehabitatHR (Calenge and Fortmann-Roe, 2013). We confirmed that forest cover (open, young, medium, and old forest) covariate values within circular buffers of GPS-tagged owls did not differ from values calculated within corresponding KDE polygons (paired t-tests, all $p > 0.05$, Table S2).

Using federal boundary maps, we classified landownership of territories entirely within national parks, national forests, or private lands accordingly. Remaining territories occurred on two ownerships; after calculating the ratio of landownership at such territories, those with a ratio between the first and third quartiles (0.31 and 0.76, respectively) were classified as "mixed-ownership". Territories with a ratio outside the quartiles were classified as the dominant owner. Thus, owl territories were assigned one of five ownership categories: national parks ($n = 35$), private lands ($n = 25$), national forests ($n = 36$), national park–national forest mixed ownership ($n = 6$), and private–national forest mixed ownership ($n = 40$).

Table 1
Definition and ranking of covariates included in isotopic mixing models to quantify spotted owl habitat–diet relationships. "QMD" abbreviates quadratic mean diameter. "LOO" abbreviates leave-one-out cross-validation results, where lower values indicate higher predictive capability.

Covariate	Definition	LOO
Hardwoods	Mean basal area of live hardwoods in a buffer	460.8
Elevation	Elevation (m) of territory center	472.6
Latitude	Latitude (°) of territory center	487.7
Medium forest[A]	Forest with QMD 30–61 cm and canopy cover > 40%	491.1
Forest heterogeneity[B]	Shannon's index calculated for the four cover types: $H = \sum_{i=1}^{s} (p_i) \times \ln(p_i)$	493.4
Young forest[A]	Forest with QMD < 30 cm and canopy cover > 40%	495.2
Null	No covariate included	496.4
Old forest[A]	Forest with QMD > 61 cm and canopy cover > 40%	498.3
Open area[A]	Land cover with canopy cover < 40%	498.8

[A] Unit is proportion of pixels in territory buffer.
[B] Unitless index.

2.4. *Data analyses*

2.4.1. *Proportional diet*

Based on remains in regurgitated pellets, flying squirrels, woodrats, and pocket gophers *Thomomys* spp. were the only prey that each constituted > 5% of biomass-corrected owl diet, and collectively constituted ~94% of biomass-corrected owl diet (Table S3). These prey were the only groups included in isotopic analyses because including infrequently consumed resources can bias proportional diet estimates (Phillips et al., 2014). We implemented K-nearest-neighbor randomization tests (Rosing et al., 1998) to establish that prey isotopic signatures did not vary regionally (all $p > 0.05$). Additional KNN tests indicated that woodrats ($n = 35$) and pocket gophers ($n = 30$) were isotopically indistinguishable ($p = 0.50$) but were distinct from flying squirrels ($n = 35$) individually and when grouped ($p < 0.001$), resulting in two isotopically distinct prey groups: (i) woodrats and pocket gophers and (ii) flying squirrels. We note, however, that between woodrats and pocket gophers, owl consumption of the former is more spatially variable and, at times, accounts for a majority of owl diet (e.g., Munton et al. (2002) found that whereas pocket gophers consistently accounted for 10–15% of biomass-corrected owl diet, woodrats represented > 80% in some landscapes and < 10% in others). Thus, we had a priori evidence that observed variability in the woodrat–pocket gopher prey group was largely due to woodrats.

We employed MixSIAR Bayesian mixing models (Stock et al., 2018) to quantify proportional diet. We corrected for trophic discrimination ($\delta^{13}C \pm$ sd: 1.88‰ ± 0.04; $\delta^{15}N \pm$ sd: 4.12‰ ± 0.26) based on snowy owl *Bubo scandiacus* captive-feeding trials (Robillard et al., 2017). After trophic correction of prey isotopic signatures, nearly all owl isotopic signatures fell within the mixing space, suggesting that we adequately sampled prey and applied appropriate trophic discrimination factors (Fig. S1A). For each model, we specified generalist ("uninformative") priors and ran three Markov chains (length = 300,000; burn-in = 200,000; thinning rate = 100). We specified process × residual error structure for all models except those containing factors with 1 level (the individual model, see below), for which only process error was estimated (Stock et al., 2018). We considered Gelman-Rubin diagnostic ($\widehat{R}$) values < 1.05 to indicate model convergence.

To assess habitat–diet relationships, we included habitat covariates in a set MixSIAR models (one covariate per model; Table 1; see Stock et al., 2018 for model-fitting details). We used leave-one-out (LOO) cross-validation to identify which covariate(s) better-predicted proportional diet than a null model.

We also included individual and territory as fixed factors in MixSIAR models and calculated medians of posterior distributions for subsequent analyses. Although this approach ignored uncertainty associated with each posterior distribution, the high Pearson correlations between median values and both upper ($r_{\text{ind}} = 0.76$, $r_{\text{terr}} = 0.85$) and lower ($r_{\text{ind}} = 0.92$, $r_{\text{terr}} = 0.94$) credible interval bounds indicated that resulting estimates of diet were largely unbiased and subsequent relationships would hold at the bounds of credible intervals.

Finally, we included territory ownership as a fixed factor in a MixSIAR model and tested for dietary differences using two-sided pairwise measures of overlap between posterior distributions of mixing model solutions (see Hopkins et al., 2014 and Manlick et al., 2019 for details). Such tests are analogous to *t*-tests; significance was evaluated at $\alpha = 0.05$.

2.4.2. Diet–space use associations

We used least-squares regression to model home range size (95% KDE polygon area [ha]) as a function of individual diet (proportion of woodrats and pocket gophers). Before interpreting model output, we ensured that assumptions of linear regression were met (i.e., normal residuals, constant variance, no influential points [all Cook's distances < 1.0]).

2.4.3. Occupancy models

We used a simple multi-season occupancy model (MacKenzie et al., 2003) to assess whether diet – and proxies for diet (prey habitat, elevation) – could explain territory occupancy dynamics. Using the best-available spotted owl detection histories across a range of landownerships and ecological conditions ($n = 73$ territories with occurrence data for various intervals between 1993 and 2017; see Appendix 2 for details), we first determined that detection probability (p) varied among surveys within years ($w = 0.99$) but not among years ($w \leq 0.001$). Then, holding initial occupancy (ψ_1) constant and colonization (γ) in a year-varying structure, we modeled territory extinction probability (ε) as a function of (i) hardwoods, (ii) elevation, and (iii) dietary proportion of woodrats and pocket gophers (all covariates were z-standardized). We used AIC to evaluate support for models relative to each other and to a null model.

3. Results

We found strong evidence that spotted owl diet was related to local habitat conditions: six covariates outperformed a null model, the best of which was the mean basal area of hardwoods in an owl territory (Fig. 2, Table 1). This variable (hardwoods) was positively associated with the estimated dietary proportion of woodrats and pocket gophers (Fig. 2A) and tended to be more abundant within territories on private lands than national forests and parks (Table S1). Elevation, latitude, medium forest, young forest, and heterogeneity of forest types also outperformed the null model (Table 1, Fig. 2).

At the local scale, spotted owl home range size significantly decreased as individual consumption of woodrats and pocket gophers increased ($\beta_{\text{WR-PG}} = -3185.4$, 95% CI $= -4855.30$ to -1515.48; Fig. 3A). Territory extinction probability (ε) was also significantly lower when owl diet contained a greater proportion of woodrats and pocket gophers ($\beta = -0.47$, 95% CI $= -0.76$ to -0.18; Fig. 3B). Moreover, hardwoods ($\Delta\text{AIC} = 7.25$) and elevation ($\Delta\text{AIC} = 9.19$) poorly explained extinction probability relative to proportional diet ($w = 0.94$; Table S4). Home range size and extinction probability results based on proportional diet were corroborated by significant positive relationships between both response variables and raw isotopic values (δ^{13}C, i.e., consumption of flying squirrels; Fig. S2).

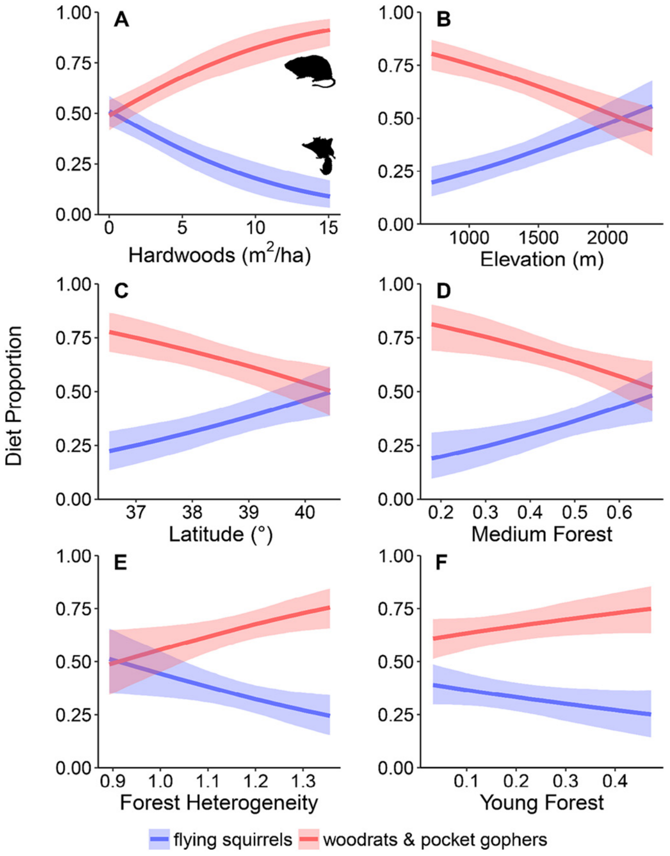

Fig. 2. Relationships between spotted owl habitat and proportional diet estimated by isotope mixing models. Only covariates that performed better than a null model based on leave-one-out cross-validation are included here. Forest class covariate units are proportions of owl territories.

At the landscape scale, spotted owls occupied divergent trophic niches among landownerships. Owls on national parks and private lands consumed significantly more woodrats and pocket gophers than did owls on national forests (Fig. 4). Moreover, comparison of diet at geographically paired national forests and national parks (Sierra NF and Sequoia-Kings Canyon NP) revealed strong trophic differences, where owls on the latter consumed significantly more woodrats and pocket gophers ($p < 0.001$; Fig. S3). Diet of owls with mixed-ownership territories generally fell intermediate to primary ownership groups (Fig. S4B).

4. Discussion

Our results suggest that trophic interactions contribute to spotted owl population differences among landscapes with contrasting land management and habitat conditions. Specifically, the consumption of presumably high-quality prey – which varied with habitat conditions – appeared to benefit spotted owls at both local and landscape scales. Although prey consumption has previously been linked to variation in spotted owl life-history traits (e.g., Zabel et al., 1995; Franklin et al., 2000), our findings are the first to show that it has consequences for territory occupancy dynamics and appears associated with landscape-scale population metrics such as density and trends in abundance. Our study also corroborates mounting evidence that (i) Eltonian niches are more plastic than previously recognized (Terry et al., 2017; Manlick et al., 2019) and (ii) trophic interactions can mediate species response to anthropogenic habitat changes (Narango et al., 2018), thus

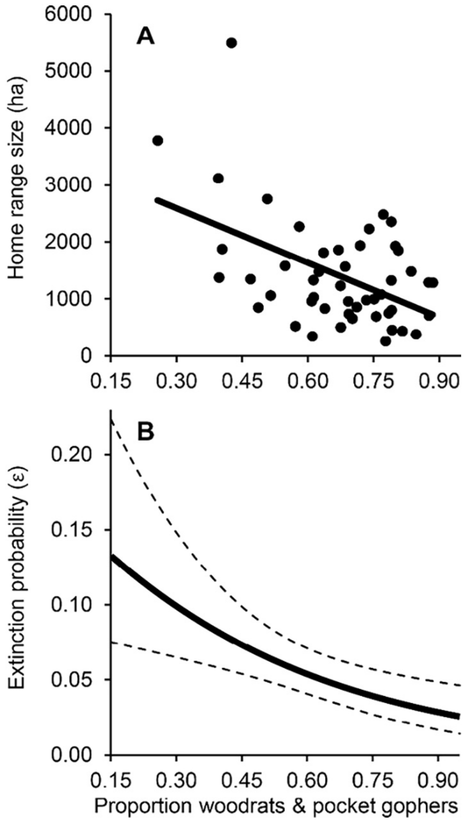

Fig. 3. Relationships between the proportion of spotted owl diet comprised of woodrats and pocket gophers and (A) home range size and (B) territory extinction probability. Thick lines indicate best fit, thin lines represent 95% CI bounds, and points indicate individual owls.

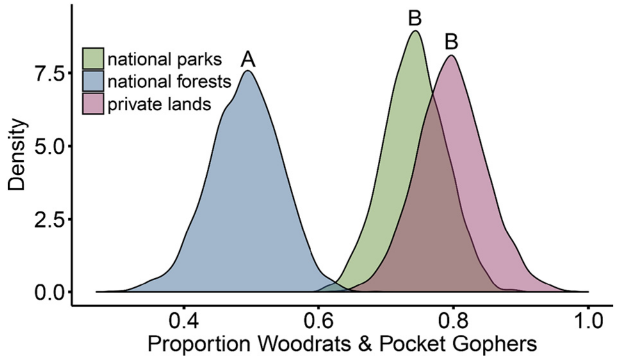

Fig. 4. Frequency distributions of proportional diet for spotted owls inhabiting the primary landownerships studied here. Letters above distributions indicate significant differences according to a two-sided test of overlap (α = 0.05).

supporting the concept that consideration of trophic interactions – in addition to habitat conditions – is important to the conservation of predator populations (Stier et al., 2016).

Our diet analyses were based on stable isotopes, which offer space- and time-integrated estimates of proportional biomass assimilation but depend on at least two key assumptions (Phillips et al., 2014). First, because consumers may utilize resources not included in mixing models, it is possible that our estimates of proportional diet are confounded with the consumption of other prey (Phillips et al., 2014). The direction and magnitude of any such biases depends on the functional roles, isotopic signatures, and dietary importance of prey not included in mixing models. In our study system, predation of primary consumers (e.g., chipmunks) by owls may result in the overestimation of woodrats and pocket gophers, predation of secondary consumers or mycophagous prey (e.g., voles) may result in the overestimation of flying squirrels, and predation of omnivorous prey with isotopic signatures intermediate to our two prey groups (e.g., *Peromyscus* spp.) may not introduce any biases in diet estimations. However, independent diet information (from regurgitated pellets) provided a measure of confidence that we included all major spotted owl prey groups in our isotopic analyses. Indeed, woodrats, pocket gophers, and flying squirrels constitute ~94% of owl diet by biomass (Table S3). Still, owls consume small amounts of other prey, so our dietary estimates of woodrats, pocket gophers, and flying squirrels must be considered relative. Nevertheless, we consider comparative differences and directional relationships to be meaningful. Second, processes other than food consumption may affect isotopic assimilation (e.g., body condition, prey digestibility, isotopic routing; Bearhop et al., 2002). However, our sample sizes were large and spanned a broad gradient of ecological conditions such that among-individual variability in such factors was unlikely to introduce a systematic bias in dietary estimates. Thus, stable isotopes appeared well-suited to quantify trophic interactions in our study system.

Isotopic mixing models provided strong evidence for relationships between habitat and prey consumption in spotted owls. In agreement with our predictions and earlier pellet-based analyses (Munton et al., 2002), owls consumed more flying squirrels in areas with prevalent medium-aged forest, at higher elevations, and at higher latitudes. Conversely, owls consumed more woodrats and pocket gophers at territories containing more hardwoods and young forest, higher forest heterogeneity, and at lower elevations – habitat features particularly important to the distribution of dusky-footed and big-eared woodrats. Thus, prey utilization varied predictably with habitat features important to flying squirrels and woodrats, but not pocket gophers (Waters and Zabel, 1995; Innes et al., 2007). This suggests that, in general, woodrats contributed more to spotted owl diets than pocket gophers (Munton et al., 2002; but see below). These findings also suggested that owls select woodrats and flying squirrels over other prey, but also that the relative consumption of these species varies, at least in part, according to availability. We recognize, however, that a lack of prey availability data precluded the distinction between selective versus proportional use of resources (Macarthur and Pianka, 1966). Regardless, our findings supported the notion that predators shift their diet in response to local habitat conditions which, in turn, may drive spatial variability in predator behavior and population status (Moss et al., 2016b).

At the individual-scale, consumption of high-quality resources leads to the utilization of smaller home ranges, which reduces energetic expenditures and predation risk (McNab, 1963). Here, we found that for the spotted owl, a central place forager, individuals that consumed more woodrats and pocket gophers had smaller home ranges (Fig. 3A). Past studies reported similar results (Zabel et al., 1995), suggesting that consumption of woodrats and pocket gophers – and particularly the former given they are large-bodied and locally high-density – may optimize foraging-related energetic expenditures. Although a formal assessment of optimal foraging in spotted owls is hampered by a lack of information on, for example, prey handling times (Macarthur and Pianka, 1966), variability in home range sizes may nonetheless be associated with energetic consequences for individual owls.

We found a novel relationship between spotted owl occupancy dynamics and prey use: territory extinction probability was lower when owls consumed more woodrats and pocket gophers, indicating that owls were less likely to die at or abandon territories where such prey was readily consumed, presumably owing to energetic benefits. Of note, the extinction–diet relationship was strongly supported despite including diet as a static, site-level covariate in occupancy models, thus assuming that resource utilization did not vary temporally. Although this assumption was likely violated to some degree, we suggest that diet is more spatially than temporally variable because (i) we found that diet varies strongly as a function of habitat conditions, which themselves have remained reasonably stable over the course of our study (Jones et al., 2018) and (ii) pellet-based data suggest that dietary proportions were relatively stable over a 25-year window in the Eldorado National Forest (B.K. Hobart, *unpublished data*). Future research that includes trophic information as a dynamic covariate (i.e., year-varying) may provide new insights into the importance of temporal variability in trophic interactions for territory occupancy of spotted owls. Regardless, because extinction probabilities drive site occupancy for long-lived species with high site fidelity such as the spotted owl, this result suggests that future shifts in prey species distributions (e.g., with climate change; Moritz et al., 2008) may cause concomitant changes in spotted owl population abundance and occupancy dynamics (Jones et al., 2016). Our results and findings by others (e.g., Chamberlain et al., 2005; Garces-Restrepo et al., 2019) indicate that trophic interactions can be an important determinant of spatial variability in population status. Thus, failure to account for such interactions in applied ecological research may lead to knowledge gaps and, at worst, ineffective or detrimental conservation measures (Stier et al., 2016).

Long-term research of spotted owls has elucidated numerous associations between occupancy dynamics and habitat conditions but few of the mechanisms that underlie those observed patterns (reviewed in Roberts, 2017). In particular, the prevalence of old forest in national parks and young forest with hardwoods in private-dominated areas explained favorable population metrics in such landscapes relative to national forests (Jones et al., 2018; Hobart et al., 2019). However, our finding that owls consumed significantly more woodrats and pocket gophers in national parks and private lands than in national forests provides preliminary evidence that trophic interactions between spotted owls and their prey may be partly responsible for differences in population abundance and occupancy dynamics among these three landscapes.

Although the historical loss of nesting and roosting habitat is one factor limiting spotted owl populations on national forests (Jones et al., 2018), forest management leading to an overreliance on relatively low-quality flying squirrels may also contribute to and exacerbate downward population trends. It is possible that forest densification and homogenization resulting from fire suppression have increased the abundance of suitable habitat for flying squirrels but not woodrats and pocket gophers (Collins et al., 2017). Bottom-up shifts in prey communities may have then altered spotted owl trophic interactions, with consequences for home range size, occupancy dynamics, and population trends. We acknowledge the alternative explanation that such downward trends could also be due to declines in flying squirrel abundance from historical levels. However, owl consumption of flying squirrels increased with medium forest – which has likely become more common on national forests owing to large-tree logging and fire suppression – suggesting that reductions in flying squirrel availability may not limit owl populations in such landscapes. A second alternative hypothesis is that rodenticides originating at illegal marijuana growing operations – which could be more common on national forests than other ownerships – are poisoning owls in such landscapes, leading to lower survival, reproduction, and territory occupancy (Gabriel et al., 2018). However, flying squirrels, which rely heavily on lichens and hypogeous fungi (Meyer et al., 2005), likely experience lower exposure to rodenticides than woodrats and pocket gophers. Thus, it is unlikely that contaminant exposure explains the relatively estimated high extinction rates at territories where spotted owls consume high proportions of flying squirrels.

In contrast to national forests, a greater reliance on woodrats and pocket gophers by spotted owls in national parks and private lands may contribute to relatively high owl abundance and occupancy rates in such landscapes. On private lands, even-aged forest management may promote patches of young forest woodrat habitat (Sakai and Noon, 1993), particularly when landowners manage for the retention and recruitment of hardwood species (e.g., California black oak) and shrub cover (Innes et al., 2007; Gray et al., 2019). Although private lands have long been thought to provide only modest suitable habitat for spotted owls owing to active logging operations (Bias and Gutiérrez, 1992), such land management may benefit owls by providing key prey resources if younger forests with shrubs and hardwoods are juxtaposed with ample nesting and roosting habitat (older forest).

Spotted owls in national parks consumed a high proportion of woodrats and pocket gophers despite a relative paucity of habitat features (e.g., young forest and hardwoods at low elevations) that our stable isotope analyses suggested promoted consumption of these two species (Table S1). By using coarse remote-sensed landcover data, we may not have captured fine-scale habitat characteristics important to pocket gophers (e.g., small meadows) and woodrats (e.g., patchy understory brush) in national parks. Such conditions are likely promoted by the prescription of frequent, low-intensity fire regimes in the national parks studied here (Collins et al., 2017). Moreover, because bushy-tailed woodrats den in rocky areas like talus slopes (which are relatively common in the national parks studied here; S.L. Roberts *personal communication*) and in cavities of large trees, it is possible that naturally-occurring geological features and the protection of defect trees in national parks acted to increase the availability of woodrats to owls. Thus, although some uncertainties remain, our results provided a plausible mechanism to explain landscape-scale variability in spotted owl population measures and suggest that incorporating information about trophic interactions is an important prerequisite to understanding how predators respond to habitat differences among landscapes with contrasting land use histories and strategies.

Our results collectively suggest that restoration and management activities that promote key prey species may also benefit predator conservation, even if prey habitat does not necessarily reflect predator habitat (e.g., nesting areas). For example, forest management in the Sierra Nevada that produces woodrat and pocket gopher habitat may also benefit spotted owls. Specifically, promoting patches of brushy woodrat habitat and grassy pocket gopher habitat adjacent to closed-canopy forests could enhance foraging opportunities for spotted owls. Our results also point to linkages among forest management, restoration, and species conservation: the regeneration of hardwoods – which has slowed owing to fire suppression – following natural and anthropogenic disturbance may simultaneously benefit woodrats, spotted owls, and forest restoration. Moreover, all three woodrat species nest and den in tree cavities, underscoring the potential benefits of forest management and restoration that retain and promote snags and trees with cavities — key structural features that have declined significantly from historical levels owing to the selective harvesting of large trees (Collins et al., 2017). Thus, as is increasingly being recognized for a range of taxa in diverse ecosystems (Samhouri et al., 2017), our research on trophic interactions suggests that compatibility may exist between ecosystem restoration in the Sierra Nevada and the conservation of the spotted owl.

More broadly, our work highlights the importance of biotic interactions as drivers of species' responses to land use and management. Consider, for example, the dramatic and ongoing decline of woodland caribou *Rangifer tarandus caribou* in North America, driven by both bottom-up (loss of lichen food resources owing to logging; Bergerud, 1974) and top-down (expansion of predators following the construction of industrial linear features; Latham et al., 2011) trophic interactions. Thus, our research and that of others suggests that failure to incorporate information about trophic interactions into species management may lead to undesirable outcomes and conservation conflicts (Stier et al., 2016). Indeed, interactions among members of ecological communities (e.g., predation) shape the role and stability of populations in novel ecosystems. Considering biotic interactions is thus likely to be important to emerging conservation issues such as reintroduction (Carlson et al., 2014) and rewildling efforts (Alston et al., 2019), climate-driven spatial (Kudrna et al., 2008) and temporal (Jara et al., 2019) shifts, and species invasions (Larson et al., 2010). Because the consequences of novel or decoupled trophic interactions extend beyond populations to both communities and ecosystems (Estes et al., 2011), incorporating the Eltonian niche is broadly valuable to applied ecological research.

Our research provides both impetus and direction to quantify linkages between anthropogenic change, trophic interactions, and population processes in other ecological systems. Despite the historical difficulty of measuring trophic interactions (Rosado et al., 2016), our stable isotope approach offers a potentially tractable avenue to quantify such relationships more broadly for three reasons. First, isotopic analyses require small quantities of biomaterials that can generally be collected with relative ease as part of ongoing ecological studies, from museum collections, or from harvested individuals. Second, recent developments have provided flexible, robust statistical tools to analyze isotopic data (e.g., MixSIAR, used here) and well-documented best practices for isotopic research (Ben-David and Flaherty, 2012; Layman et al., 2012; Phillips et al., 2014). Third, isotopic information can be combined with additional, potentially preexisting data (e.g., behavioral, occupancy, fitness, or demographic) to improve and augment understanding of how biotic interactions affect species. Our two-step approach demonstrated that the benefits of modern isotopic analyses can be leveraged to (i) identify how trophic interactions vary with habitat conditions and (ii) identify the consequences of changes in trophic interactions for a focal species. However, this approach is not limited to questions about linkages among habitat, diet, and population processes, but could be used to study how trophic interactions mediate population responses to invasions, extinctions, light and noise pollution, disturbance, and climate change. Although such relationships are seldom tested explicitly, doing so could help elucidate previously unrecognized and cryptic mechanisms by which species respond to environment change.

Declarations of Competing Interest

The authors declare no conflicts of interest.

Data accessibility

The data associated with this paper have not been archived due to the sensitive legal and political circumstances surrounding the pending listing decision for the California spotted owl (*S. o. occidentalis*) under the U.S. Endangered Species Act.

Acknowledgements

We thank Philip Manlick, Jonathan Pauli, Susan Roberts, and two anonymous reviewers for insightful feedback on this research. We also thank Stephanie Eyes, Sarah Stock, Jeff Pierini, Claire Viellieux, and many field technicians for assisting the collection of data used for this research.

Author contributions

B.K.H. and M.Z.P. conceived the ideas and designed the study; all authors collected the data; B.K.H., G.M.J., and M.Z.P. drafted the manuscript with inputs from all authors. All authors contributed substantially to revisions and approved the final draft of the manuscript.

Role of the funding source

We received financial support from the USDA Forest Service Region 5, USDA Forest Service Pacific Southwest Research Station, California Department of Fish and Wildlife, and Sierra Pacific Industries. These contributions funded personnel salaries, field research, and laboratory work.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.biocon.2019.108217.

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Landscape heterogeneity provides co-benefits to predator and prey

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Words in abstract: 360

Words in manuscript: #

Number of references: 84

Number of tables: 2

Number of figures: 5

Abstract

Predator populations are imperiled globally, due in part to changes in habitat and trophic interactions. Theoretical and laboratory studies suggest that heterogeneous landscapes containing prey refuges that act as source habitats can benefit both predator and prey populations, although the importance of heterogeneity in natural systems is uncertain. Here, we tested the hypothesis that landscape heterogeneity mediates predator-prey interactions between the California spotted owl (*Strix occidentalis occidentalis*) – a mature forest species – and one of its principal prey, the dusky-footed woodrat (*Neotoma fuscipes*) – a younger forest species – to the benefit of both. We did so by combining estimates of woodrat density and survival from live-trapping and VHF tracking with direct observations of prey deliveries to dependent young by owls in both heterogeneous and homogeneous owl home ranges. Woodrat abundance was approximately 2.5x higher in owl home ranges featuring greater heterogeneity in vegetation types of mature forest, young forest, and open areas (1805.0 ± 50.2 SE) compared to home ranges dominated by mature forest (727.3 ± 51.9 SE), in large part because of high densities in young forests that appeared to act as sources promoting woodrat densities in nearby mature forests. Woodrat mortality rates were low across vegetation types and did not differ between heterogeneous and homogeneous home ranges, yet all observed predation by owls occurred within mature forests, suggesting young forests may act as woodrat refuges. Spotted owls exhibited a type 1 functional response, consuming approximately 2.5x more woodrats in heterogeneous (31.1/month ± 5.2 SE) versus homogeneous (12.7/month ± 3.7 SE) home ranges. While consumption of smaller-bodied alternative prey partially compensated for lower woodrat consumption in homogeneous home ranges, owls nevertheless consumed 30% more prey biomass in heterogeneous home ranges – approximately equivalent to the energetic needs of producing one additional offspring. Thus, a mosaic of vegetation types including young forest patches increased the abundance and availability of woodrats that, in turn, provided energetic and potentially reproductive benefits to mature forest-associated spotted owls. More broadly, our findings provide strong empirical evidence that heterogeneous landscapes containing prey refuges can benefit both predator and prey populations. As anthropogenic activities continue to homogenize landscapes globally, maintaining heterogeneous systems with prey refuges may benefit imperiled predators.

Keywords: Forest management, heterogeneity, predator-prey, spotted owl, woodrat

1 | Introduction

Predator populations are declining globally, often precipitated by habitat loss and changes in trophic interactions (Estes et al. 2011, Ripple et al. 2014). Many predators occur, and presumably evolved, in complex landscapes with heterogeneously distributed resources that shape many of their ecological interactions (Hunter and Price 1992, Wiens 1995). Among these, the composition and configuration of habitat patches can mediate predator-prey interactions, with consequences on population dynamics for both predator and their prey (Schmitz 1998, Fahrig et al. 2011, Wilson et al. 2019). As anthropogenic land-use change increasingly homogenizes landscapes, there is a growing need for empirical studies on the effects of heterogeneity (variability of an environmental property in time and space; Li and Reynolds 1995) in predator-prey systems (Layman et al. 2007, Bullock et al. 2022). However, to date most studies of the effects of heterogeneity on predator-prey interactions have been theoretical or conducted within controlled experimental settings subject to many simplifying assumptions (Hastings 1977, Sih 2005). Further, empirical studies are typically conducted at patch rather than landscape scales, do not involve mobile predators capable of accessing many patches, or fail to account for alternative prey (Ryall and Fahrig 2006).

Landscape heterogeneity is most likely to affect predator-prey dynamics through effects on prey abundance or vulnerability. In heterogeneous systems, landscape-scale abundance of prey is an emergent property of the composition of habitat patches of varying quality, with landscapes containing a greater area of high-quality habitat patches expected to have higher prey abundance (Holt 1985, Iles et al. 2018). However, dispersal from high-density source patches can increase densities within lower-quality patches (Holt 1985), decoupling local abundance from habitat quality (Ehrlén and Morris 2015, Iles et al. 2018). In some cases, landscape-scale abundance may even exceed the combined carrying capacity of all representative patches (Holt 1985, Zhang et al. 2017). When predation rate is determined by prey density (i.e., the functional response), these patch- and landscape-scale differences in prey abundance can have profound effects on predator populations (Holling 1959, Coulson et al. 2006), which may be most pronounced when predators exhibit differential hunting success among patches (Hopcraft et al. 2005).

Landscape heterogeneity can affect prey vulnerability by creating refuges that reduce predation risk – i.e., the likelihood of a predator encountering or capturing prey (Sih 1987). When predator and prey prefer different habitats, the relative amounts and arrangements of safe (difficult for the predator to successfully capture prey) versus risky (easier for the predator to successfully capture prey) patches can decouple prey availability from abundance (Hebblewhite et al. 2005, Laundré 2010), with ostensible tradeoffs when either habitat type predominates. Homogeneous landscapes dominated by risky habitat may increase prey accessibility but limit abundance or advance prey depletion (Huffaker et al. 1963, Coulson et al. 2006), while landscapes dominated by safe habitat may increase prey abundance but limit capture opportunities (Hopcraft et al. 2005).

By reducing top-down control on prey abundance, refuge use can also promote density-driven dispersal into adjacent risky patches (Holt 1985) and provide foraging opportunities along the edges of the two habitat types (Laundré and Hernández 2003, Zulla et al. 2022). Therefore, compared to homogeneous landscapes where predator habitat predominates, heterogeneity may decrease the availability of hunting patches for predators but increase the encounter probability within those that remain, potentially increasing hunting success (Hopcraft et al. 2005, Zulla et al. 2022). In summary, the relationship between habitat characteristics and predation rates often depends on the landscape context, although needed are studies conducted across a gradient of heterogeneity in natural systems – i.e., complex landscapes containing a mosaic of prey refuges and patches of varying density and catchability *versus* homogeneous ones dominated by a single habitat type and uniform catchability of prey.

We assessed how landscape heterogeneity mediates predator-prey interactions between a mature-forest predator, the California spotted owl (*Strix occidentalis occidentalis*) and one of its primary prey species, the dusky-footed woodrat (*Neotoma fuscipes*). While spotted owls consume a variety of small mammals and other taxa, woodrats represent the largest-bodied (Ward Jr et al. 1998), and thus most energetically profitable prey when present (Weathers 1996). As such, woodrat consumption can drive patterns in fitness, occupancy, and space use for spotted owls (Franklin et al. 2000, Hobart et al. 2019a). Spotted owls use mature forest for nesting, roosting, and foraging (Gutierrez et al., 1995), while woodrats are predominantly associated with younger, brushier forests and large oaks (Williams et al. 1992, Sakai and Noon 1993) that are traditionally viewed as less suitable habitat for foraging owls (Atuo et al. 2019, Kramer et al. 2021a). Despite this purported mismatch between predator and prey habitat, in lower-elevation forests of the Sierra Nevada, USA, woodrats can comprise up to 94% of spotted owl diet by weight (Williams et al.

1992). Sakai and Noon (1997) observed intermittent, short-distance movements into mature forests from woodrats occupying dense young forests within a patchy landscape, suggesting that forays across ecotonal boundaries may increase the vulnerability of woodrats to avian predation. Indeed, recent work has linked increasing forest heterogeneity at a home range scale to woodrat consumption (Hobart et al. 2019a), and documented frequent woodrat captures by owls foraging along edges between hardwood and coniferous-dominated forests (Zulla et al. 2022). In the Sierra Nevada, differences in management practices among landownership types has created landscapes that differ dramatically in forest composition and patch configuration (North et al. 2017), providing a gradient of heterogeneity to examine (i) the mechanisms driving increased woodrat consumption by spotted owls and (ii) determine whether these mechanisms also confer benefits to woodrat populations at a landscape scale.

Herein, we hypothesized that heterogeneous landscapes would create sources or spatial refuges for prey that benefit both predator and prey populations when predators and prey are associated with different habitats. We combined live-trapping and monitoring of woodrat survival with direct observations of prey deliveries by spotted owls to test several predictions related to our central hypothesis. Specifically, we predicted (1) owl home ranges with greater habitat heterogeneity, in the form of a mosaic of vegetation types including mature forest, young forest, and open areas, would contain higher densities of woodrats than homogeneous home ranges consisting primarily of mature forest. We also predicted

(2) mortality rates of woodrats would be higher in mature forest and within homogeneous home ranges because of the lack of young forest refuges, but (3) a functional response exists where owl predation rates on woodrats would be higher in heterogeneous than homogeneous home ranges. Finally, we predicted (4) total biomass of prey delivered to owl nests would be greater in

heterogeneous home ranges because of a greater consumption of large-bodied woodrats and, accordingly, the consumption of alternative, smaller-bodied prey would not reconcile this deficit in homogeneous home ranges.

2 | Methods

2.1 | Study system

Our study primarily occurred on the western slope of the central Sierra Nevada, CA, USA, within and adjacent to the Eldorado Demography Study Area (EDSA; Figure 1), a long-term spotted owl monitoring site encompassing roughly 355 km^2 of the Eldorado National Forest (Jones et al. 2021). Elevation in the EDSA ranged from 366 to 2,257 m, although we concentrated our woodrat trapping efforts within approximately 1,000 to 1,500 m, a range that can contain dense woodrat populations (Williams et al. 1992). Dominant conifer species included incense cedar (*Calocedrus decurrens*), ponderosa pine (*Pinus ponderosa*), sugar pine (*P. lambertiana*), Douglas fir (*Pseudotsuga menziesii*), and white fir (*Abies concolor*), while dominant hardwoods included California black oak (*Quercus kelloggii*) and tanoak (*Lithocarpus densiflorus*), the latter of which was patchily distributed throughout the study area in dense pockets (Fites-Kaufman et al. 2007).

Landownership in the EDSA was split between ~60% public land, primarily managed by the United States Forest Service (USFS), and ~40% private land, existing mostly as commercial timberlands. Differences in land use practices among ownership types in this region have created a landscape with distinct spatial variation in forest structure, age, and configuration. On USFS-managed lands, a century of clearcutting and selective logging of large trees, coupled with extensive fire suppression, has created contiguous, spatially homogeneous stands of mature trees within public forests (Stephens et al. 2015). On privately-owned lands, timber harvesting occurs more frequently, often with an emphasis on even-aged management that creates a mosaic of different stand types including open clear cuts, young plantations interspersed with brushy pockets of saplings and tanoak, and patches of mature forest similar to those occurring on public lands (North et al. 2017). Forests on private lands are on average 30-40 years younger than those on public lands and may contain less stand features generally found in older forests, such as large snags and logs (Stewart et al. 2016). Thus, private lands tend to contain forests with less vertical structure, but more heterogeneity in forest ages, including young stands that can harbor dense woodrat populations (Sakai and Noon 1993). Spotted owls nest and forage on both ownership types (Roberts et al. 2017, Hobart et al. 2019b, Atuo et al. 2019).

2.2 | Overview

To test our predictions about the effects of landscape heterogeneity on predator-prey interactions between spotted owls and woodrats we: (1) used live-trapping and mark-recapture methods to estimate woodrat abundance (prediction 1); (2) deployed very high frequency (VHF) collars on woodrats to monitor individual survival and identify causes of mortality (e.g., likely owl predation; prediction 2); and (3) quantified consumption rates by monitoring woodrat and other prey deliveries to nests with video cameras within owl home ranges (predictions 3 and 4). All three of these field methods were conducted in home ranges containing varying degrees of habitat heterogeneity.

2.3 | Classifying landscape composition and configuration within spotted owl home ranges

We compared occupied spotted owl home ranges that were either highly homogeneous or heterogeneous in the proportional composition and configuration of open, young, and mature forest (see below for definitions). To identify homogeneous or heterogeneous home ranges for woodrat sampling, we visually inspected aerial imagery from the National Agriculture Imagery Program (NAIP) at all known spotted owl home ranges (*n* = 28) within and immediately adjacent to the EDSA and identified ones containing predominantly mature forest in large, contiguous stands versus those that had a more even mixture of open, young, and mature forest of differing patch sizes (Figure 2A, B).

For this subset of highly homogeneous and heterogeneous home ranges, we created circular buffers with a 2.12 km radius – an area equal to the median home range of all males tagged for a minimum of 25 days (1,412 ha) from previous studies (Jones et al. 2016, Atuo et al. 2019, Zulla et al. 2022) – around the most recent known nest or roost site. Next, within each buffered home range, we used NAIP imagery collected in 2018 and 2020 to manually digitize patches of relatively uniform vegetation conditions following protocols described in Tempel et al. (2014). We defined the three predominant forest structure classes based on canopy cover and size of dominant trees as follows: mature forest (>40% canopy cover and dominant trees >12 inches diameter at breast height [dbh]), young forest (>40% canopy cover and saplings or dominant trees <12 inches dbh), and open habitat (<40% canopy cover). Heterogeneous home ranges had more even representation of habitat types, estimated by Shannon's diversity index ($\hat{H}$ = 0.92, range = 0.79 – 1.05; mean areas = 58.8% mature, 27.9% young, and 12.2% open) than homogeneous home ranges ($\hat{H}$ = 0.65, range = 0.57 – 0.71; mean areas = 78.6% mature, 9.9% young, and 11.5% open).

For tests of woodrat abundance and survival (predictions 1 and 2), we excluded home ranges that were far away from other home ranges we considered sampling, above elevations with high woodrat densities (>1,500 m) and below elevations where owls are commonly found in our study landscape (<1,000 m), or predominantly within the King Fire footprint and likely confounded substantially by severe fire (Jones et al. 2016). From the remaining subset, we then selected 9 home ranges (5 homogeneous; 4 heterogeneous) by prioritizing ones that were occupied at the time of woodrat sampling based on routine spotted owl surveys conducted as part of the EDSA (Jones et al. 2021), occurred at similar elevations (mean elevation range 1290-1372 m), and occurred in close proximity. For tests of prey delivery rates by owls (predictions 3 and 4), we selected 4 of these home ranges along with an additional 11 from the EDSA and Sierra Pacific Industries' Stirling Study Area (SSA) in the northern Sierra Nevada (Zulla et al. 2022). Among these, home ranges had similar representation of habitat types compared to those from predictions 1 and 2, with greater evenness in heterogeneous (H = 0.99 range = 0.82 – 1.05; mean areas = 54.3% mature, 27.9% young, and 17.8% open)than homogeneous home ranges (H = 0.71, range = 0.62 – 0.74; mean areas = 76.4% mature, 10.9% young, and 12.7% open).

2.4 | Field methods and analysis

Prediction 1: Estimating woodrat abundance

To compare woodrat abundance within homogeneous and heterogeneous home ranges, in 2020 and 2021 we deployed grids of 64 traps (in 8x8 or 4x16 configuration) spaced at 50 m intervals among eight of the nine occupied spotted owl home ranges classified as homogeneous (*n* = 4) or heterogeneous (*n* = 4; Figure 1). Within homogeneous home ranges, we randomly placed grids within large stands of contiguous mature forest (Figure 2C). Within heterogeneous home ranges, we deployed trapping grids stratified by habitat – using ArcMap and NAIP imagery where, specifically, we created an algorithm to identify edge areas between young-mature and open-mature patches of a minimum size to center our trapping grids. We centered our trapping grids along habitat edge to ensure adequate representation of core and edge for each habitat type; variable patch size and distribution in heterogeneous home ranges posed challenges to sampling (e.g., uneven representation of habitat types) if we followed a truly random grid placement strategy

(Figure 2B). As part of this process, we constrained grid locations such that they contained at least 30% each of mature forest and either young forest or open area (Figure 2C).

We deployed traps for six consecutive days following a paired approach in which two grids were sampled concurrently – one each within a heterogeneous and homogeneous home range. Trapping occurred from late spring through summer in 2020 and 2021. We captured woodrats in steel mesh traps (model #105; Tomahawk Live Trap Company, Hazelhurst, Wisconsin, USA) baited with a mix of birdseed, dried fruit, and peanuts. All captured animals were ear punched and marked with a unique ear tag (Model 1005-1; National Band & Tag Company, Newport, KY) or passive integrated transponder (PIT) tag (Avid Identification Systems, Norco, CA). All captures were done with approval by the Institutional Animal Care and Use Committee of the University of Wisconsin, Madison (IACUC #A006173-A01), and followed guidelines from the American Society of Mammalogists (Sikes et al. 2019).

We estimated abundance using Huggins closed-capture models in program MARK (White and Burnham 1999). We modeled initial capture probability (p) and recapture probability (c) accounting for time (i.e., sampling occasion), sampling year, habitat type (open, young, mature), and home range configuration (heterogeneous or homogeneous). For model selection, we used Akaike's Information Criterion corrected for small sample size (AICc) and AICc weights (w) to select the best-supported model and assessed significance using 95% CIs. If a competitive model contained one or more uninformative parameters (i.e., parameter CIs overlapped zero), we dropped this model from consideration (Arnold 2010). We then used our top model to derive woodrat abundance for each habitat type.

To estimate relative densities by habitat type, we applied these abundance estimates to the effective trapping area (ETA) surveyed (Gerber and Parmenter 2015). We estimated ETA (in km^2)

following Parmenter et al. (2003); in this, we buffered all grids by 50 m, equal to half of the estimated mean for maximum nightly distance moved by woodrats, then summed the total area of each habitat type captured across all buffered grids. Then we calculated density estimates for each habitat type by dividing the model-derived abundance estimates by its respective ETA (Schwemm et al. 2018). Given that dispersal from patches of adjacent young forest may facilitate increased woodrat densities (Sakai and Noon 1993, 1997), we considered mature forest in heterogeneous and homogeneous home ranges as two separate habitat classes. We obtained estimates for woodrat abundance within homogeneous ($\hat{N}_H$) and heterogeneous ($\hat{N}_E$) home ranges by scaling up our density estimates relative to the area of open (A_O), young (A_Y), and mature (A_M) forest within each home range (see Supporting Information Appendix S1). Statistical comparisons of abundance between homogeneous and heterogeneous home ranges were performed using a two-sample Welch's *t*-test.

Prediction 2: Estimating woodrat survival

To test prediction 2, we monitored survival with radio-transmitters and assessed cause-specific mortality. We selected a subsample of the woodrats caught within seven of the eight occupied spotted owl home ranges (3 homogeneous; 4 heterogeneous) during our mark-recapture surveys from Prediction 1, along with other individuals trapped opportunistically among these and one additional homogeneous home range, for survival monitoring. In 2020 and 2021, we fit woodrats weighing above 120g with VHF collars (Lotek model TW-5, 10g; Lotek Wireless Inc, Newmarket, Ontario, Canada or Telenax model TXE-116C, 6g; Titley Scientific, Columbia, Missouri, USA) equipped with onboard activity sensors, which allowed us to detect mortality events shortly after they occurred. Within 2 days of collar deployment, we tracked individual woodrats to their nests (hereafter "middens") and recorded relevant information about each area. We assigned habitat designations (open, young, mature) for every collared individual based on where the midden was located, not where they were trapped – although these were typically the same habitat type.

We initiated VHF monitoring in 2020 on the week of 14 June and in 2021 on the week of 11 May. We located collared woodrats 1-2 times per week, and recorded status (alive, dead, missing/collar failure) on each occasion from the first capture until death, disappearance, or the end of the study (17 October 2020 or 11 September 2021). We also performed monthly midden checks – repeating triangulation of collared woodrats to middens - to ensure that an individual had not permanently dispersed during our monitoring period. If a signal for a woodrat collar disappeared, we set traps outside of their midden for several days. In all but one incident, the source of the lost signal was a dead collar battery – in these cases, the individual was recaptured alive, the collar was removed, and monitoring ended.

Once an inactive signal was detected we immediately recovered the collar. We recorded images and took detailed notes for each mortality event, including location, habitat type, distance to midden, and state of collar to assess cause of mortality. Avian predation was considered the cause of death if the collar was recovered with minor damage under a spotted owl nest tree or perch site with whitewash and/or viscera in the vicinity; while other raptor species were present in our study area, we attributed avian predation to spotted owls given that all sites were owl-occupied, mortalities occurred at night, and all recovered collars were found in close proximity to active spotted owl nest sites. Additionally, woodrats are the most common spotted owl prey and are rarely consumed by other predators of a similar size class (e.g., red-tailed hawk *Buteo jamaicensis*). Mammalian predation was considered the cause of death if the collar was recovered in more open, brushy habitat absent of any roosting or perching trees, with considerable damage and teeth marks to the collar. Finally, if the collar was tracked to a midden with a mortality signal active, we set traps for several days to ensure that the collar was not malfunctioning and the individual was not alive – after which it was determined to be a mortality of unknown or of natural cause (e.g., age, nutritional deficiency, disease) and not a predation event.

We estimated weekly woodrat survival rates by constructing known-fate models in Program MARK (White and Burnham 1999), with a staggered entry design to allow introduction of individuals throughout the study (Pollock et al. 1989). We analyzed two sets of known-fate models: one considering all mortality events, and one only including mortalities that were attributed to avian (likely spotted owl) predation. In 2020 we constructed encounter histories from 14 June until 17 October; in 2021 we constructed encounter histories from 9 May until 11 September. We set Sunday as the start of each sampling week and introduced covariates relative to habitat type, home range composition, month, year, distance to owl nest tree or territory center, and considered a categorical effect relative to each unique home range.

Prediction 3: Estimating woodrat consumption rates by owls

We directly observed prey deliveries to dependent young by nesting spotted owls within home ranges classified as either homogeneous or heterogeneous. We used GPS tagging and nest-video monitoring data collected and described previously by Zulla et al. (2022). Briefly, in 2019 and 2020 breeding spotted owls were located as part of ongoing work within the EDSA and SSA (Roberts et al. 2017, Hobart et al. 2019b, Zulla et al. 2022), and 15 nesting males were captured and GPS tagged (5 in 2019; 10 in 2020). Infrared video cameras (AXIS Q1786-LE 4; Axis communications AB, Lund, Sweden) were placed at nest sites of these individuals, secured to an adjacent tree with a clear view of the nest. These cameras continuously recorded high-quality video throughout the nocturnal foraging period (20:00-06:30 PDT). All video footage was reviewed and prey deliveries to the nest were identified to species whenever possible. We detected 26 larger-bodied prey deliveries over the course of monitoring that could not be identified to species; these were split relatively evenly among homogeneous and heterogeneous sites, and we do not believe that excluding these from our count of woodrat deliveries compromised any results. We estimated woodrat delivery rates (number delivered per hour) and scaled these to monthly estimates. We conducted a two-sample Welch's *t*-test to determine differences in mean monthly woodrat delivery rates between homogeneous and heterogeneous home ranges.

We corroborated the above-described estimates of monthly woodrat consumption rates in homogeneous and heterogeneous home ranges by multiplying per-capita mortality rates (prediction 2) with woodrat abundance estimates (prediction 1). We then conducted a two-sample Welch's *t*-test to test for differences in monthly woodrat consumption rates between homogeneous and heterogeneous home ranges. We corroborated these estimated mortality rates with those derived from nest camera data by conducting a one-way ANOVA with two factors: estimation method (nest camera or known-fate estimates) and landscape composition (heterogeneous or homogeneous). This allowed us to determine whether the number of monthly woodrat mortalities differed between our methods of estimation.

Prediction 4: Estimating biomass delivery rates by owls

To estimate total biomass delivery rates (grams per unit time), we used nest video data described in prediction 3 and considered all prey deliveries. To convert number of prey items into biomass rates, we used mean values for body mass of each prey item collected and described in Zulla et al. (2022). Briefly, mean values for mass of woodrats and Humboldt flying squirrels (*Glaucomys oregonensis*) were estimated using regurgitated pellets collected from previous studies in the EDSA. Skull and mandible measurements of skeletons from these pellets were compared to those of museum specimens for which masses were available, and predictive relationships between mass and skull measurements were quantified to determine estimates of body mass for each skeleton collected from pellets. Estimated mean body mass of woodrats was 187.4 g (range 110.9 - 271.2) and flying squirrels was 98.8 g (range 80.2 - 117.2). Other prey species were assigned a mass based on the midpoint of mass ranges in the literature (e.g., mouse 20g; Reid 2006). Finally, if species of a prey delivery could not be determined, then it was assigned to a size class (extra small; 5.3g, small; 47.5g, medium; 175g, large; 205g) with corresponding mass derived from the average mass of species within this size class.

We summed deliveries of all species or size classes and converted these into biomass values, then standardized them to biomass delivery rates (g delivered per hour) and scaled these to monthly estimates. We also conducted two-sample Welch's *t*-tests to determine if there were differences in delivery rates of each prey group and total biomass delivery between homogeneous and heterogeneous home ranges.

3 | Results

Prediction 1: Higher woodrat abundance within heterogeneous home ranges

Over the two field seasons, we deployed 22 grids of 64 traps each among eight spotted owl home ranges (4 heterogeneous, 4 homogeneous) for a total of 8,448 trap nights and captured 236 unique individuals a total of 460 times. Our most supported mark-recapture model for woodrat abundance suggested a behavioral response to capture, as p = 0.12 (95% CI: 0.07, 0.20) and c = 0.33 (95% CI: 0.30, 0.37), with neither parameter varying as a function of sampling year, habitat type, or landscape composition. Several other models occurred within 2 $\mathrm{AIC_c}$, yet all included uninformative parameters (Arnold 2010) so were deemed noncompetitive (Table 1).

Woodrat density was greatest in young forest (215.3 woodrats/km^2; 95% CI: 156.0, 359.0), followed by mature forest in heterogeneous home ranges (134.2 woodrats/km^2; 95% CI: 97.9, 220.0), mature forest in homogeneous home ranges (57.8 woodrats/km^2; 95% CI: 42.0, 95.7), with the lowest densities in open area (9.5 woodrats/km^2; 95% CI: 5.8, 31.2; Figure 3). Extrapolating woodrat density estimates relative to the area of each habitat type within owl home ranges, woodrat abundance was approximately 2.5x higher ($t_6 = 14.92$, $p < 0.001$) in heterogeneous home ranges ($\hat{N}_H = 1{,}805.0$ woodrats; range: 1,662.3 – 1,897.8) than homogeneous home ranges ($\hat{N}_O = 727.3$ woodrats; range: 648.9 – 817.9).

Prediction 2: Higher woodrat mortality within mature forests and homogeneous home ranges

We radio-collared and monitored 108 woodrats (35 in 2020; 73 in 2021) within 8 owl home ranges (4 heterogeneous; 4 homogeneous) and compiled a total of 1,030 weekly monitoring records. Collars were deployed evenly among three of the four habitat classes (37 mature-homogeneous; 36 mature-heterogeneous; 35 young). Woodrats were not collared in open areas given the low densities that occurred in this vegetation type. We observed minimal dispersal over the survey period. During monthly checks, only two individuals moved to a different midden with an average dispersal distance of 90 m and neither of these individuals dispersed to a different habitat type. We confirmed 12 mortalities over the course of our study: 3 from avian (and presumably spotted owl) predation, 3 from mammalian predation, and 6 from non-predation events.

The top model for woodrat survival contained only an intercept, indicating that woodrat survival rates did not vary by landscape composition, among habitat types, or year. Models including covariates for sampling year and habitat type were within 2 AIC_c, yet involved uninformative parameters (Arnold 2010) so were deemed noncompetitive (Table 2). Weekly woodrat survival relative to all mortality sources was low ($\hat{s} = 0.988$; 95% CI: 0.980, 0.993), while weekly survival relative to avian (likely spotted owl) predation alone was even lower ($\hat{s} = 0.997$; 95% CI: 0.991, 0.999). While we did not detect an effect of habitat on survival rates, all three mortalities from avian predation occurred within mature forest (2 mature-heterogeneous; 1 mature-homogeneous).

Prediction 3: Greater woodrat consumption by owls in heterogeneous home ranges

We monitored 15 nesting owl pairs over 115 days for 1173.3 total monitoring hours. One camera was removed from analysis due to limited deployment duration (10.5 hours). We confirmed 306 prey delivery events and identified 243 deliveries to species. Of these, we identified 93 individual deliveries of woodrats (i.e., 30.4% of all deliveries of known species) to owl nestlings. From the video-based nest delivery data, we estimated a consumption rate of 22.8 woodrats per month (95% CI: 13.5, 34.5) across all home ranges, with greater monthly consumption in heterogeneous ($\bar{x} = 32.4$ woodrats/month; 95% CI: 19.2, 48.8) versus homogeneous ($\bar{x} = 13.3$ woodrats/month; 95% CI: 5.2, 25.4) home ranges ($t_{12} = 1.84$, $p = 0.09$; Figure 4), significant at the 0.1 but not 0.05 level. Based on our combined data from predictions 1 and 2, we estimated an average mortality rate relative to avian (likely spotted owl) predation of 20.2 woodrats per month (95% CI: 14.1, 26.4) across all home ranges, with a greater number of monthly mortalities in heterogeneous ($\bar{x} = 28.8$ woodrats/month; 95% CI: 27.2, 30.0) versus homogeneous ($\bar{x} = 11.6$ woodrats/month; 95% CI: 10.2, 13.0) home ranges ($t_6 = 14.94$, $p < 0.001$; Figure 4). This corroborated estimates from nest camera data, as there were no significant differences in woodrat consumption rates in homogeneous or heterogeneous home ranges between estimation methods (ANOVA: $p = 0.71$).

Prediction 4: Greater biomass delivery by owls within heterogeneous home ranges

In addition to woodrats, we confirmed deliveries of 90 flying squirrels, 30 *Peromyscus* spp., 4 voles, 2 pocket gophers, 2 moles, 1 bird, and 1 bat among the 306 confirmed deliveries. Another 63 deliveries were not identified to species but were grouped into size class to allow for biomass estimates; of these, 9 were extra small, 19 were small, 9 were medium, and 26 were large. The remaining 20 prey deliveries were not categorized into size classes. While woodrat consumption was much greater among spotted owls occupying heterogeneous home ranges (see above), we found no effect of landscape composition on the delivery frequency of flying squirrels ($t_{12} = 0.14$, $p = 0.89$) or all other alternate prey combined ($t_{12} = 0.80$, $p = 0.44$; Figure 5A). Accordingly, flying squirrel biomass was similar in heterogeneous ($\bar{x}$ = 2705.9 g/month) versus homogeneous ($\bar{x}$ = 2553.6 g/month) home ranges. Further, while spotted owls consumed an additional 1,000 g/month of other prey in homogeneous ($\bar{x}$ = 3,176.1 g/month) versus heterogeneous ($\bar{x}$ = 2,139.6 g/month) home ranges (Figure 5B), this difference was not enough to compensate for the 2.5x greater consumption of woodrat biomass in heterogeneous ($\bar{x}$ = 6,055.6 g/month) versus homogeneous ($\bar{x}$ = 2,485.8 g/month) home ranges. Specifically, owls delivered total biomass at a rate 1.3x greater (2,685.6 more g/month) in heterogeneous ($\bar{x}$ = 10,901.1 g/month) versus homogeneous ($\bar{x}$ = 8,215.5 g/month) home ranges (Fig 5B).

4 | Discussion

We demonstrated that landscape-scale heterogeneity in vegetation types including young forest refuges increased the abundance and availability of woodrats that, in turn, provided energetic and potentially reproductive benefits (see below) to mature forest-associated spotted owls – thus providing strong empirical support for the hypothesis that prey refuges can benefit predators in heterogeneous landscapes. While previous theoretical and laboratory-based research has suggested that landscape heterogeneity including patches of prey refuges can profoundly affect predator-prey dynamics, these approaches typically involve highly simplified conditions, are conducted at patch rather than landscape scales, or fail to account for alternative prey (Ryall and Fahrig 2006, Juliano et al. 2022). Thus, our findings provide some of the first evidence from natural systems that promoting landscape heterogeneity may provide co-benefits to both predator and prey populations and constitute an effective strategy for conserving endangered predators.

Young forests promote woodrat abundance within heterogeneous landscapes

As predicted, woodrat abundance was approximately 2.5x greater in heterogeneous than homogeneous spotted owl home ranges, in large part because of greater woodrat densities in young forests that were more prevalent in heterogeneous home ranges. The finding that woodrat densities in young forests were considerably greater than in mature forests was consistent with previous studies (Sakai and Noon 1993, Ward Jr et al. 1998), as were low densities in open areas with little vegetation cover (Cranford 1977). Young forest confers likely benefits to woodrat populations by providing higher quality food resources owing to a greater diversity and abundance of flora (Carraway and Verts 1991, Sakai and Noon 1993), a more stable microclimate (Atsatt and Ingram 1983), structures and materials required for nest building (Innes et al. 2007), and cover that reduces predator risk (see also below) (Sakai and Noon 1997). High woodrat densities in young forest, whether the result of resource availability or reduced predation, may have supported woodrat populations in nearby mature forests as evidenced by the 2.3x greater densities we estimated for mature forests within heterogeneous compared to homogeneous home ranges (Figure 3). Indeed, high densities and associated intraspecific competition in young forest patches may lead to increased dispersal, from these source populations that recruit into lower density mature forest patches (Sakai and Noon 1997, Hansen et al. 2019), a process expected to be weaker in homogeneous spotted owl home ranges containing less young forest.

Counter to our predictions that woodrat survival rates would be greater in young forests and heterogeneous (prey-dense) home ranges, we observed no difference in survival among vegetation or landscape types, either overall or from presumed spotted owl predation. This result contrasts with a previous study that found lower survival within mature forest patches, likely due to higher predation rates from spotted owls (Sakai and Noon 1997). However, mortality rates were uniformly very low, both overall and from spotted owl predation, which may have limited our ability to detect differences in survival rates among vegetation or landscape types statistically. Of note, all presumed spotted owl predation events observed in this study occurred in mature forest: 1 in mature homogeneous and 2 in mature heterogeneous – similar to observations by Sakai & Noon (1997). As such, the balance of evidence indicates that young forests, to a degree, act as woodrat refuges from spotted owl predation. However, young forests almost certainly harbored relatively high woodrat densities primarily because they provided greater resource availability given the marked difference in densities yet similar predation rates among habitat types. Spotted owl predation exerted little to no top-down pressure on woodrat populations given the very low estimated per-capita predation rates, even in mature forests - suggesting that high densities in young forests are driven as much, and likely more, by bottom-up processes.

Landscape heterogeneity promotes woodrat consumption by spotted owls

Spotted owls consumed more woodrats in heterogeneous than homogeneous landscapes, presumably because of greater woodrat abundance – with nest video monitoring and population-based approaches yielding very similar estimates of woodrat consumption rates. This finding supports previous analyses via stable isotopes that the proportion of woodrats present in spotted owl diets increases with forest heterogeneity (Hobart et al. 2019a). Spotted owls in our study exhibited a type I functional response (i.e., prey consumption rate increases linearly with prey density; Holling 1959) given they consumed 2.5x more woodrats in heterogeneous home ranges, which themselves contained a 2.5x greater abundance than homogeneous territories. The 1:1 relationship between woodrat consumption and abundance suggests that spotted owls are consuming more woodrats in heterogeneous home ranges because of higher encounter rates rather than kill rates. Regardless of the mechanism, the linear functional response indicates that vegetation management promoting woodrat populations can, under appropriate conditions, lead to direct increases in woodrat acquisition by spotted owls.

As expected, lower delivery rates of woodrats by spotted owls to their nests in homogeneous home ranges containing fewer woodrats reduced overall biomass delivery rates (Figure 5B). Further, owls in homogeneous home ranges only partially reconciled the deficit of decreased woodrat deliveries with alternative prey (Figure 5A). Thus, the "reduction" in mature forest spotted owl habitat in heterogeneous landscapes did not come at a cost to, but rather benefited, spotted owl prey acquisition. Spotted owls likely attempt to maximize energy gain by selecting prey that most efficiently balance foraging costs with the benefits of prey consumption (Stephens and Krebs 1986, Sih 2005). Reliance on smaller and less dense prey, such as flying squirrels, or very small species, such as mice, may incur costs including increased energetic expenditures associated with prey searching or reduced biomass delivery rates (Ruiz-Olmo and Jiménez 2009, Moorhouse-Gann et al. 2020). In contrast, consuming a greater proportion of larger-bodied and densely distributed prey such as woodrats can reduce these costs (McNab 1963) or increase biomass delivery rates, with benefits for occupancy, space use, and even population growth (Wendland 1984, Coulson et al. 2006, Hobart et al. 2019b).

To explore potential fitness outcomes associated with increased biomass delivery rates in heterogeneous home ranges, we estimated the energetic cost of a nesting spotted owl pair to produce and raise one, two, or three young and converted this into monthly prey biomass values based on Ward Jr et al. (1998) and Weathers (1996) (see Supporting Information Appendix S2). Based on these calculations, we estimated that spotted owls GPS-tagged in homogeneous landscapes captured and delivered enough biomass to produce and raise approximately two young, whereas owls in heterogeneous landscapes met the energetic costs of raising approximately three young (Figure 5B). While we were not able to assess whether greater prey biomass delivered to nests translated directly to fitness benefits given our sample size, food supplementation has increased reproductive performance in many avian species, including owls, in controlled experiments (Korpimäki 1992, Ruffino et al. 2014). Thus, we consider it likely that prior observations of higher spotted owl reproduction in heterogeneous home ranges (Franklin et al. 2000) and home ranges containing more young forest and hardwoods (Hobart et al. 2019b) were the result of greater woodrat abundance and consumption by owls, as suggested by these authors.

Conclusions and management implications

Our results suggest that promoting landscape heterogeneity could benefit spotted owl populations in parts of their range where woodrats are important prey. Heterogeneity is a natural feature of many dry forest ecosystems occupied by spotted owls, and was maintained historically by frequent and predominantly low- to moderate-severity fires and smaller high-severity burned areas resulting from natural and Indigenous sources (Anderson 2006, McLauchlan et al. 2020). These forests, then, were typically characterized by larger stands of comparatively open, but large tree-dominated forests interspersed with smaller patches of early successional shrub and young forest (Boisramé et al. 2017) that presumably harbored dense woodrat populations (Sakai and Noon 1993, Innes et al. 2007). However, more than a century of fire suppression coupled with the historic selective logging of large trees has created denser, more homogeneous forests with fewer early successional patches and large trees (North et al. 2017). Our results strongly suggest that the homogenization of these forests has reduced the abundance of woodrats and their consumption by spotted owls – and come at a cost to overall prey acquisition and potentially reproductive success. This conclusion is supported by a constellation of previous studies indicating that spotted owls: (1) forage and capture woodrats at the edge of young and mature forest (Sakai and Noon 1997, Kramer et al. 2021b, Zulla et al. 2022); (2) consume a greater proportion of woodrats in more heterogeneous landscapes based on stable isotope analyses (Hobart et al. 2019a); (3) have smaller home ranges, higher territory occupancy rates, and higher densities in areas where they consume more woodrats (Zabel et al. 1995, Hobart et al. 2019a); and (4) can have higher reproductive rates in heterogeneous landscapes including those that contain a relatively high proportion of young forest with hardwoods (Franklin et al. 2000, Hobart et al. 2019b).

As such, our findings, in conjunction with these previous studies, indicate that promoting landscape heterogeneity characterized by a mosaic of mature and young forests could help ameliorate the population declines observed in many areas by enhancing prey availability (Tempel et al. 2014, Conner et al. 2016). This can be achieved through active management that incorporates fire use and timber harvest strategies that mirror the fine-scale habitat loss and recruitment events typically supported by historical disturbance regimes (Collins et al. 2017). This continuously creates small patches of open habitat which regenerate into future young forest following planting or natural re-seeding, emulating a natural mosaic of vegetation types. By incorporating system dynamics of historically disturbance-prone forests, including those in western North America, the ‘managed dynamics’ approach to conservation can maintain both forest resilience and critical wildlife habitat (Steel et al. 2022, Gaines et al. 2022), although it requires continuous action to balance successional changes within regenerating patches (Steel et al. 2022). Our work demonstrating the benefits of heterogeneity to spotted owls, mediated by woodrat availability, was conducted in landscapes containing, in addition to national forests, privately-owned lands managed for commercial timber production that yield a relatively high proportion of such young forests in patches tens of acres in size. While national forests are increasingly managed with an emphasis on fuels reduction intended to restore lower-severity fire regimes, this strategy can produce stands of younger forests in small, severely burned patches only if small high-severity patches are acknowledged and planned for as a desired outcome. Thus, the current emphasis on the restoration of historical fire regimes and historical forest structure (e.g., individual trees, clumps, and openings) from active harvest and burning strategies is likely to benefit spotted owl populations by creating high density woodrat refuges adjacent to mature forest, while also reducing the risk of megafires that render large areas unsuitable for spotted owl foraging (Jones et al. 2016, 2020). Our work provides yet further evidence that the conservation of spotted owls and promotion of forest ecosystem resilience are compatible rather than conflicting objectives (Jones et al. 2022) – a perception that has constrained forest restoration in these highly vulnerable ecosystems (Collins et al. 2010).

Our findings have implications for species and ecosystems beyond the forests of western North America as historical and contemporary land use practices have homogenized forests worldwide (Schulte et al. 2007, Collins et al. 2017, Sapkota et al. 2021). Human activities, including timber extraction, agricultural intensification, afforestation, and severe fires have created ecological patterns without historical equivalent across all forest biomes (Seastedt et al. 2008). These departures from historical landscape conditions can alter the availability, predictability, and distribution of resources (Ullmann et al. 2018), and is increasingly recognized as a global threat to biodiversity and ecosystem function, particularly among species adapted to naturally complex ecosystems (Riley et al. 2003, Anile et al. 2019). For predators, landscape simplification can cause declines in prey diversity and abundance (Cramer and Willig 2002, Benedek and Sîrbu 2018), with consequences for behavior, space use, and demography (Parsons et al. 2022). However, despite the fact that species at higher trophic levels may be most impacted by landscape-scale changes such as homogenization due to space and resource needs (Ripple et al. 2014), these effects have often been overlooked in studies of predators inhabiting human-altered environments (Ryall and Fahrig 2006). Here, we provide empirical evidence demonstrating the mechanisms whereby landscape-level processes alter prey availability to predators and explore a trophic-driven fitness consequence of landscape simplification. We recommend the promotion of management strategies that preserve and restore historical heterogeneity, and also highlight the importance of considering spatial scale, habitat associations, and predator mobility in future studies on predator-prey interactions. There is a growing drive to understand and incorporate ecological complexity within conventional restoration approaches (Bullock et al. 2022), and our results show that understanding the role of landscape heterogeneity in predator-prey dynamics can benefit predator conservation worldwide.

Acknowledgements

The U.S. Forest Service Region 5, Sierra Pacific Industries, and U.S. Forest Service Pacific Southwest Research Station funded this work. We are grateful to Byron de Yampert, Zina Lor, and Lily Olmo for their help with data collection in the field; William Berigan and Sheila Whitmore for logistical support and spotted owl expertise; Anu Kramer for assistance with spatial analyses; and staff at the Blodgett Forest Research Station for providing housing and office space during fieldwork.

Author contributions

CCK, MZP, JNP, CJZ, SCS, BPD, KNR, and JJK conceived the ideas and designed methodology; CCK and CJZ collected the data; CCK, MZP, and JNP analyzed the data; CCK and MZP led the writing of the manuscript, with key input from JNP. All authors contributed critically to the drafts and gave final approval for publication.

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Table 1. Top Huggins closed-capture models for estimating dusky-footed woodrat (*Neotoma fuscipes*) abundance in 2020 and 2021 in the central Sierra Nevada, California, USA. Information includes model covariates for initial capture probability (*p*) and recapture probability (*c*), ranked by AICc (Akaike's Information Criterion adjusted for small sample size), and compared by ΔAICc (difference in AICc between a model and the top-ranked model), *w* (model weight), and k (number of parameters).

Covariate(s)	**AICc**	**ΔAICc**	***w***	**k**
p(.), c(.)	1535.607	0.000	0.260	2
p(year), c(.)	1536.610	1.003	0.158	3
p(.), c(t)	1536.775	1.168	0.145	6
p(.), c(year)	1537.439	1.831	0.104	3
p(t) = c(t)	1537.517	1.909	0.100	6

Table 2. Top known-fate survival models for estimating dusky-footed woodrat (*Neotoma fuscipes*) survival in 2020 and 2021 in the central Sierra Nevada, California, USA. Information includes model covariates, ranked by AICc (Akaike's Information Criterion adjusted for small sample size), and compared by ΔAICc (difference in AICc between a model and the top-ranked model), *w* (model weight), and k (number of parameters).

Covariate(s)	**AICc**	**ΔAICc**	***w***	**k**
Null	132.721	0	0.319	1
Year	133.942	1.221	0.173	2
Habitat	134.241	1.520	0.149	2
Landscape	134.725	2.004	0.117	2
Year + Habitat	135.419	2.697	0.082	3

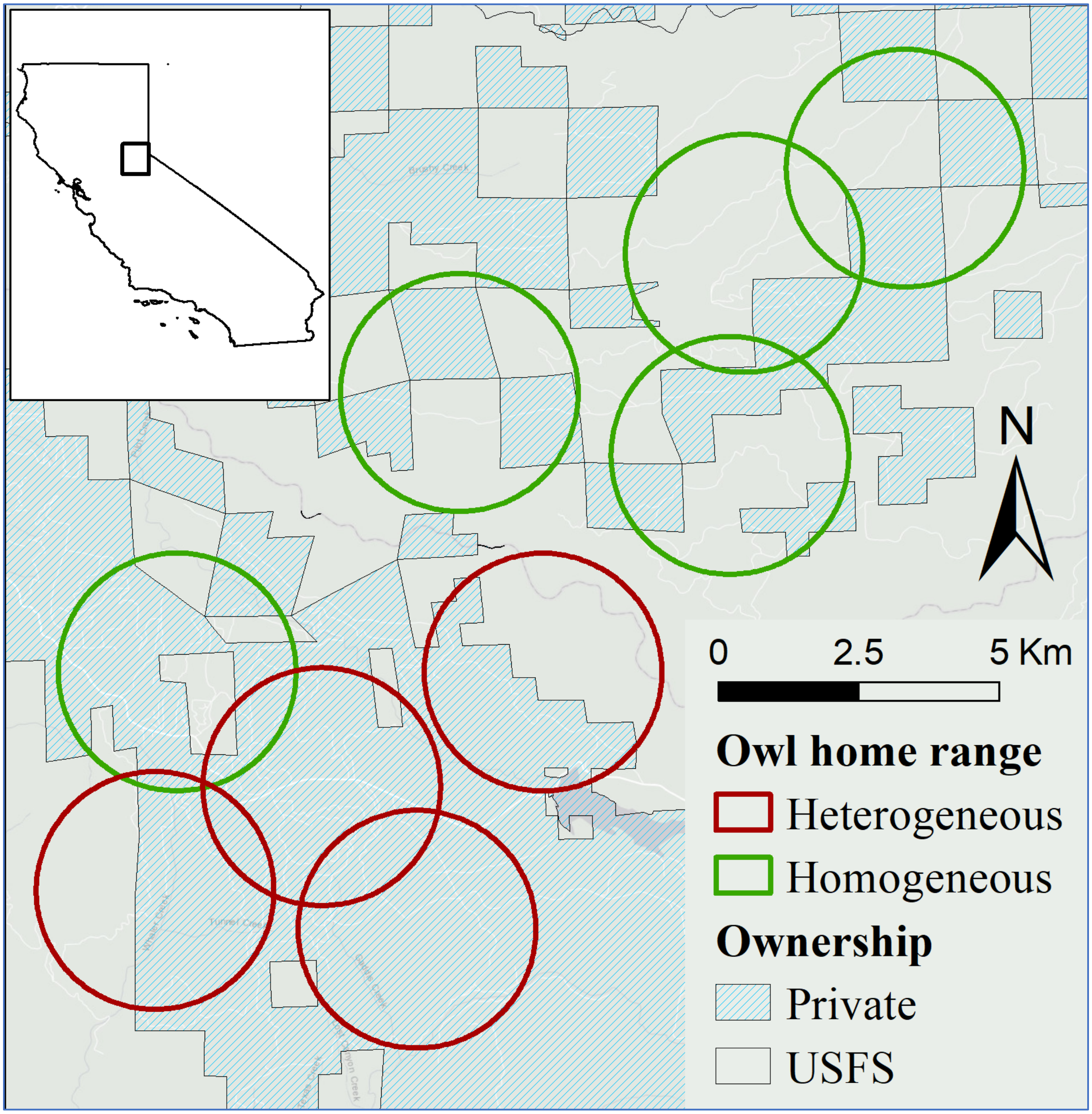
Figure 1: Locations of spotted owl (*Strix occidentalis*) home ranges within and adjacent to the Eldorado Demography Study Area (EDSA) in the central Sierra Nevada, California, USA where dusky-footed woodrat (*Neotoma fuscipes*) abundance and survival (predictions 1 & 2) were estimated in 2020 and 2021. Landscape composition is depicted by red (heterogeneous) and green (homogeneous) circles.

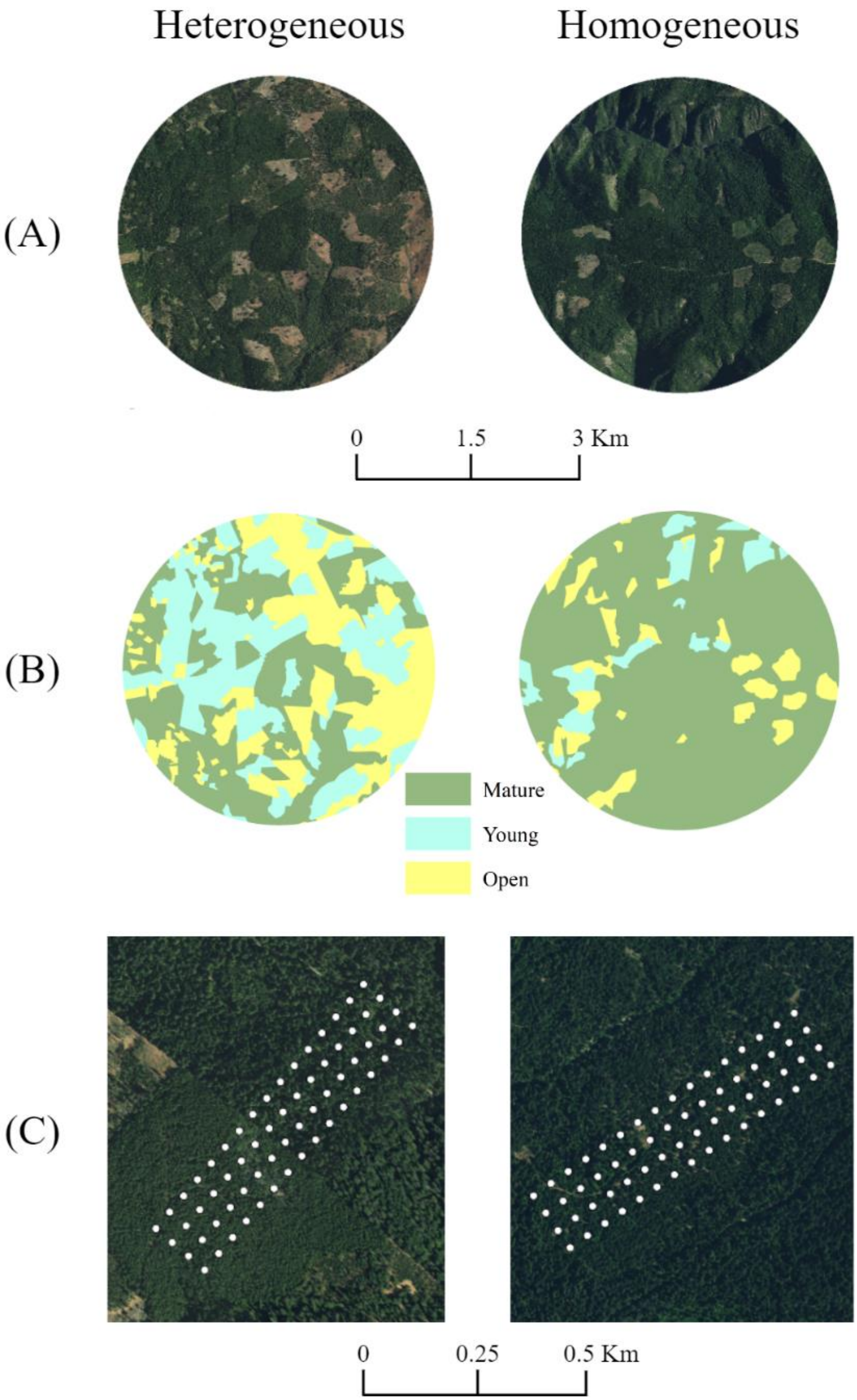
Figure 2: Examples of landscape composition (heterogeneous or homogeneous) within spotted owl (*Strix occidentalis*) home ranges surveyed in 2020 and 2021 in the central Sierra Nevada, California, USA. Differences are shown at the scale of a spotted owl home range with both (A) NAIP imagery and (B) habitat type (mature, young, and open), and (C) at the scale of a trapping grid visualized with NAIP imagery.

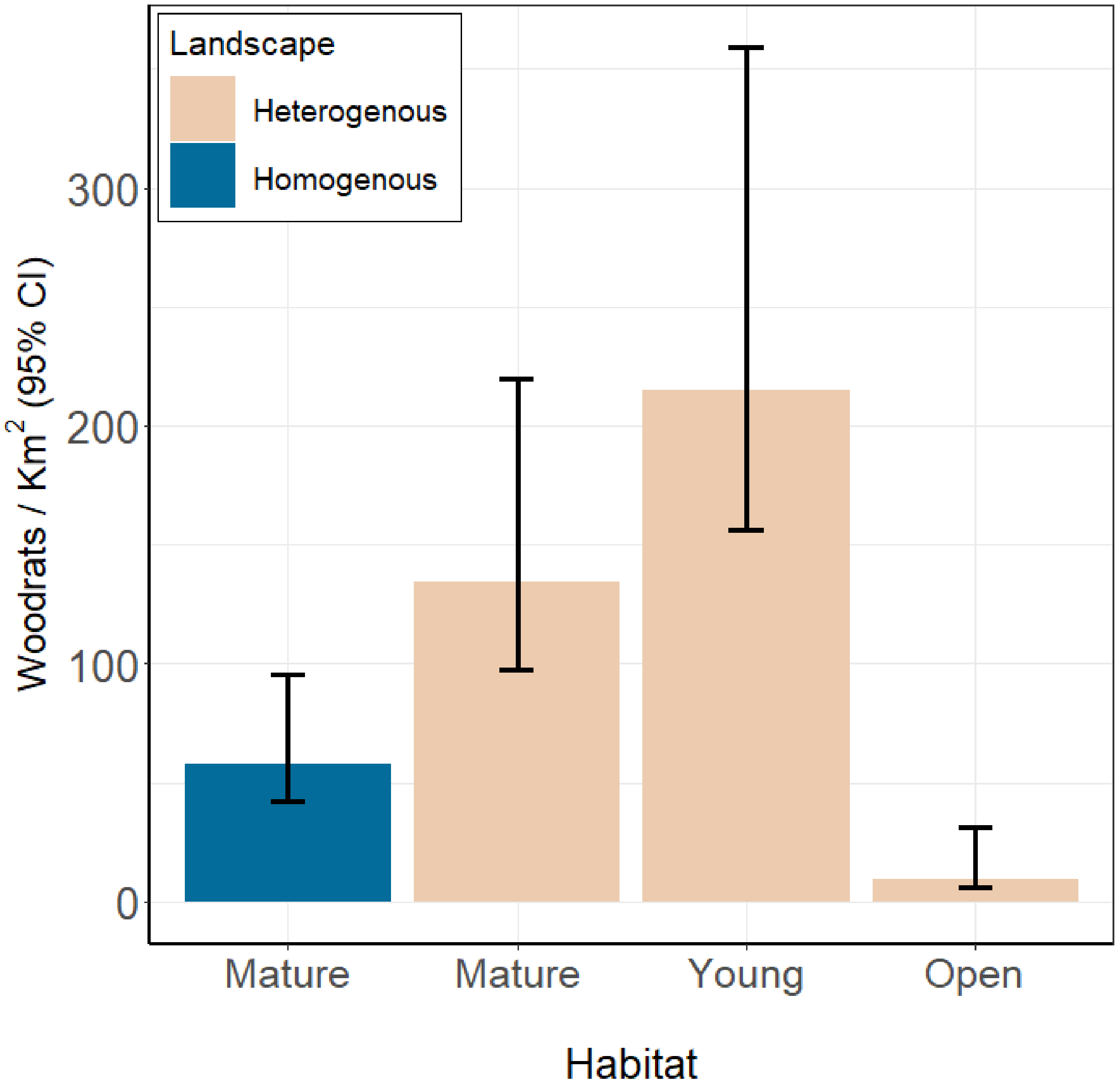
Figure 3: Estimated density (±95% CI) of dusky-footed woodrats (*Neotoma fuscipes*) in 2020 and 2021 within habitat types in the central Sierra Nevada, California, USA. Density is shown as number of woodrats per km^2 in open habitat, young forest, and mature forest within home ranges classified as heterogeneous and homogeneous.

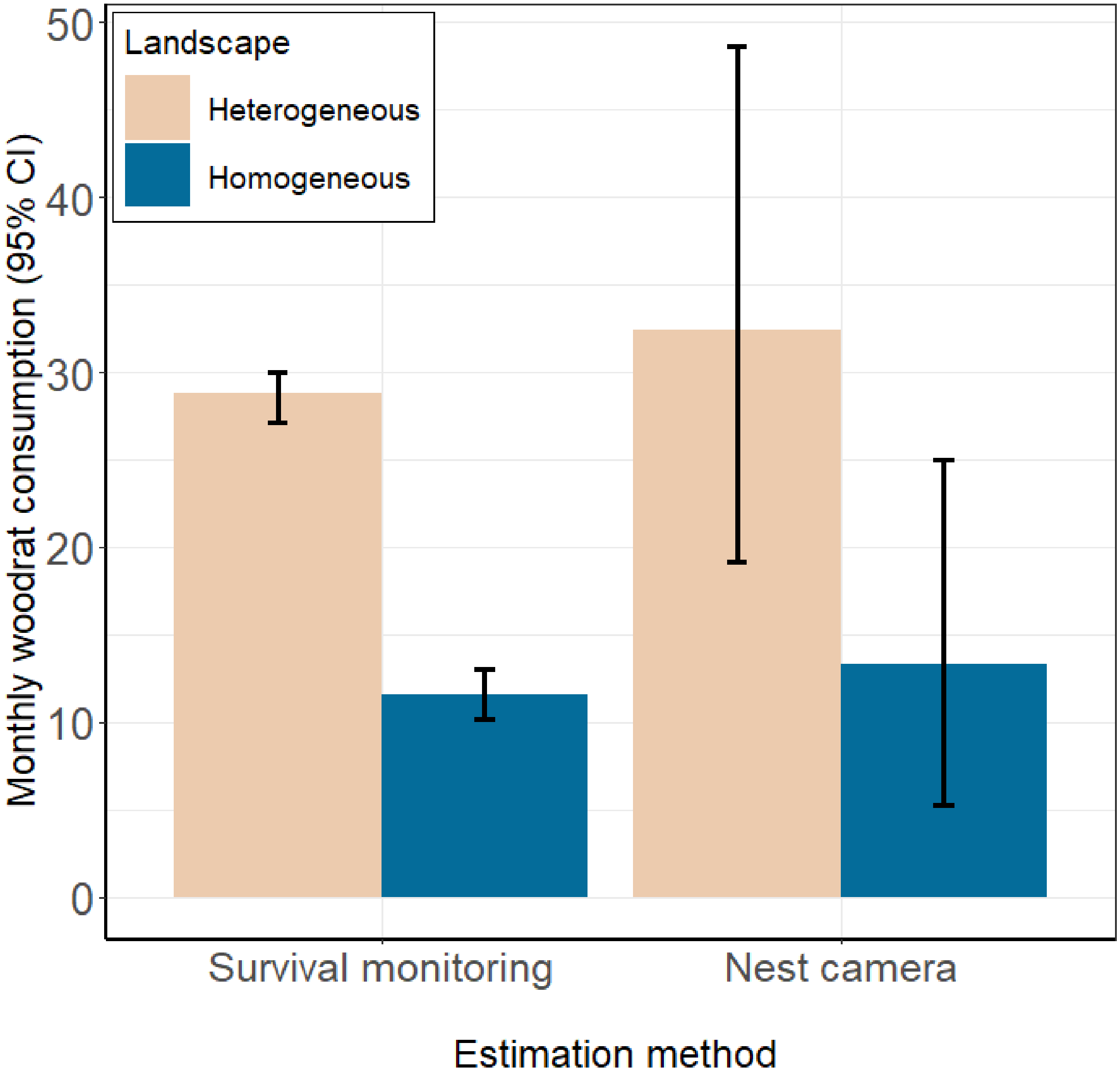
Figure 4: Estimated monthly consumption rate (±95% CI) of dusky-footed woodrats (*Neotoma fuscipes*) by spotted owls (*Strix occidentalis*) within the central and northern Sierra Nevada, California, USA, derived from monitoring and mark-recapture data (Survival monitoring) or nest camera data (Nest camera) within home ranges classified as heterogeneous or homogeneous.

Figure 5: Estimated monthly prey delivery rate by prey species (a) and biomass (b) in 2019 and 2020 by spotted owls (*Strix occidentalis*) within heterogeneous and homogeneous home ranges within the central and northern Sierra Nevada, California, USA. Horizontal dashed lines on (b) represent the estimated metabolic cost to produce and raise one, two, or three young for a nesting owl pair, derived from Ward Jr. et al. (1998) and Weathers (1996).

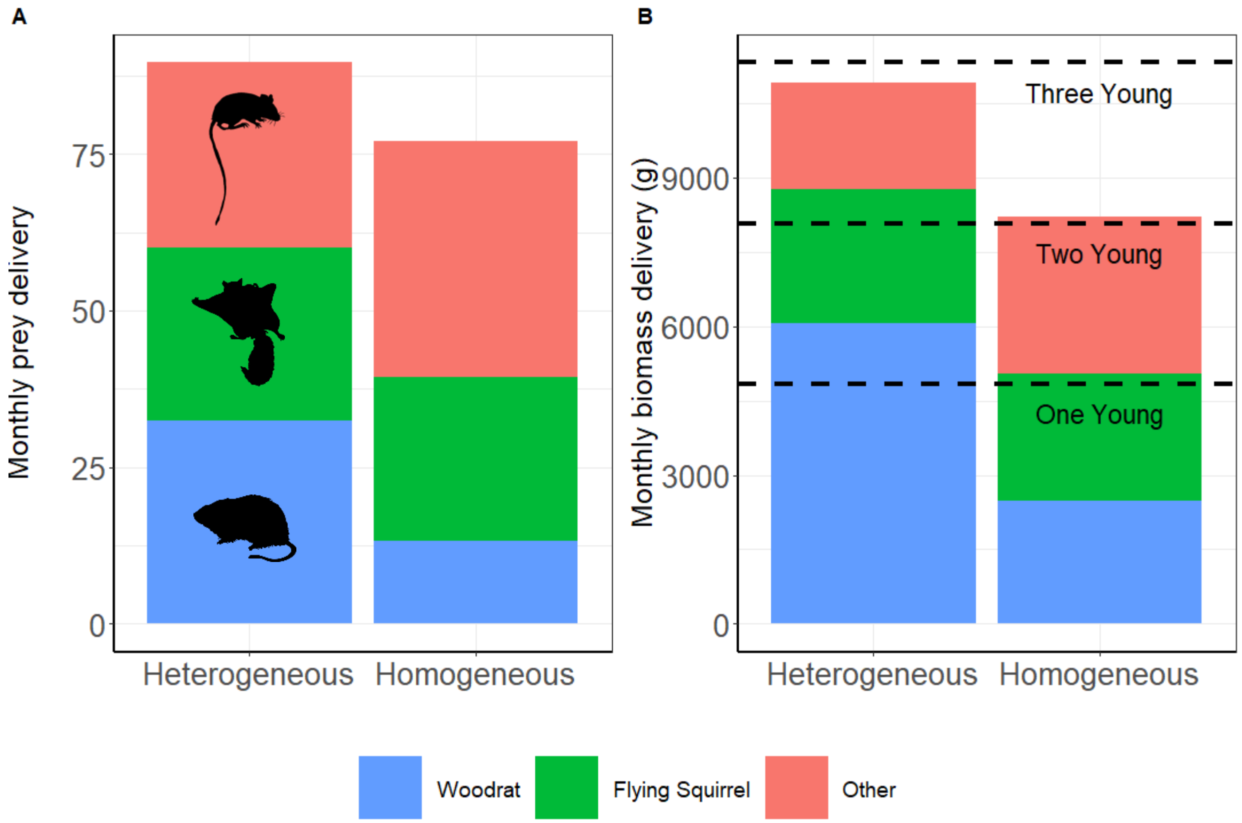

N
0
2.5
5 Km
Owl home range
Heterogeneous
Homogeneous
Ownership
Private
USFS


Heterogeneous
Homogeneous
(A)
0
1.5
3 Km
(B)
Mature
Young
Open
(C)
0
0.25
0.5 Km


Landscape
Heterogenous
Homogenous
300
200
100
0
Woodrats / Km^2 (95% CI)
Mature
Mature
Young
Open
Habitat


Landscape
Heterogeneous
Homogeneous
Monthly woodrat consumption (95% CI)
0
10
20
30
40
50
Survival monitoring
Nest camera
Estimation method

842


A
B
Monthly prey delivery
0
25
50
75
Heterogeneous
Homogeneous
Monthly biomass delivery (g)
0
3000
6000
9000
Three Young
Two Young
One Young
Heterogeneous
Homogeneous
Woodrat
Flying Squirrel
Other

Attachment D

Zulla, C.J., et al. 2022a

Attached is a copy of Zulla, C.J., Kramer, H.A., Jones, G.M., Keane, J.J., Roberts, K.N., Dotters, B.P., Sawyer, S.C., Whitmore, S.A., Berigan, W.J., Kelly, K.G., Wray, A.K., Gutiérrez, R.J., and Peery, M.Z. 2022a Large trees and forest heterogeneity facilitate prey capture by California Spotted Owls. Ornithological Applications 124(3):1-14.[1]

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[1] This study is submitted with CFA et.al. comment letter on the proposed listing of the CSO as Attachment D.

Forest heterogeneity outweighs movement costs by enhancing hunting success and fitness in spotted owls

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Research Article

Keywords: habitat fragmentation, habitat heterogeneity, hunting success, movement, reproductive output, spotted owl

Posted Date: March 18th, 2022

DOI: https://doi.org/10.21203/rs.3.rs-1370884/v1

Abstract

Context

The concepts of habitat fragmentation and heterogeneity are central to the conservation of biodiversity; yet understanding when landscapes transition from heterogenous to fragmented can challenge conservation in practice. Complex and sometimes difficult-to-measure responses of species, and ultimately biological communities, to habitat heterogeneity and fragmentation may reflect the outcome of life-history trade-offs shaped by different landscape properties.

Objectives

Here, we tested the hypothesis that a mosaic of forest stands improved hunting and breeding success for California spotted owls (*Strix occidentailis occidentalis*).

Methods

We integrated high-temporal-resolution GPS tags, video monitoring of nests sites, long-term assessments of reproductive status, and high-resolution remotely-sensed vegetation data in a mixed-ownership landscape in the Sierra Nevada, California.

Results

Spotted owls made shorter nocturnal movements when medium forest was prevalent in their territory. However, spotted owls delivered prey at a higher rate to nests sites when they had more forest edge in their territory, which presumably provided greater access to large-bodied woodrat prey. Further, spotted owl reproductive output was relatively high in territories that contained a mix of mature and open forest.

Conclusions

Thus, the benefits heterogenous forests provide to hunting success appear to outweigh costs associated with additional commuting to foraging sites and provide emergent fitness benefits to spotted owls. We suggest that the line between habitat heterogeneity and fragmentation can be a complex one that varies not only among, but within, species. Further, understanding the effects of heterogeneity and fragmentation on biological communities will require more empirical and mechanistic studies of individual species.

1 Introduction

The concepts of habitat fragmentation and heterogeneity are central to the conservation of biodiversity. Habitat heterogeneity is often defined as the occurrence of multiple habitat types distributed in a landscape mosaic of patches with different characteristics (Turner & Gardner, 2015). Habitat heterogeneity can promote species diversity by increasing partitionable niche space among species, with empirical studies demonstrating positive heterogeneity-diversity relationships in many systems (Currie, 1991; Hutchinson, 1957; Macarthur & Macarthur, 1961; Stein et al., 2014; Tews et al., 2004). By contrast, habitat fragmentation can be defined as the geographic isolation of a particular habitat type or types into small patches, most notably through human activities (Haddad et al., 2015; Taylor et al., 1993; Turner & Gardner, 2015). Such changes can cause species loss by reducing population sizes, limiting dispersal movements, and edge effects (Marini et al., 1995; Ryall & Fahrig, 2006; Saunders et al., 1991). Accordingly, ensuring that heterogenous landscapes do not exceed a threshold where they become fragmented and incur species losses has long been a guiding principle of conservation science (Andren, 1992; Boulinier et al., 1998; Ford et al., 2001; Wiens et al., 2018).

Yet, uncertainty in the relative effects of habitat heterogeneity and fragmentation on individual species and species assemblages – as well as whether those effects are beneficial or detrimental – can challenge conservation in practice. Indeed, whether a landscape should be considered “heterogenous” (typically considered a desirable condition) or “fragmented” (typically considered an undesirable condition), is complex given both involve the nature of dispersion among habitat patches. For example, should a landscape containing a mix of older and regenerating younger (e.g., from timber harvesting or severe wildfire) forest patches be considered heterogenous or fragmented from the perspective of native animal species and communities? Further, responses - whether they be beneficial or determinantal - to changes in landscape pattern will depend on the size, configuration, and the juxtaposition of patch types (Hanski et al., 2013; Loke et al., 2019; Tilman et al., 1997), which can vary among species as mediated variation in life history traits (Chesson, 2018; Crooks et al., 2017; Stein et al., 2015; Wilson et al., 2016). Highly mobile species with strong dispersal capabilities and wide niche breadths are more likely to be resilient to changes in landscape pattern that increase the dispersion among patches of different types (Emer et al., 2019; Tabarelli et al., 2012). Such variability in responses among species lead to non-positive heterogeneity-relationships that, in theory, would limit or preclude increases in biodiversity from management practices aimed at increasing habitat heterogeneity (Heidrich et al. 2020).

Whether the effects of past or future landscape change can be expected to be beneficial or detrimental is further challenged by recent research suggesting that fragmentation per se (fragmentation independent of habitat loss) can increase species diversity. In a recent review, Fahrig (2017) suggested that responses to fragmentation were typically positive, where increasing dispersion among patches of habitat often increased species diversity and benefited populations of individual species. Among proposed mechanisms, Fahrig suggested that greater habitat heterogeneity in such fragmented landscapes can benefit some species and communities, further blurring the line between habitat fragmentation and heterogeneity. Importantly however, Fletcher et al. (2018) argued Fahrig’s central premise and methods were incorrect, and that fragmentation typically increases extinction rates and decreases colonization rates (Fletcher et al., 2018). Similarly, in a synthesis of experimental evidence, Haddad et al. (2015) showed that fragmentation reduces biodiversity by 13–75%. Collectively, this scientific uncertainty, coupled with the apparent complex and variable responses of species and communities to changes in landscape pattern, challenge conservation efforts intended to promote species diversity and individual species of concern in complex landscapes.

The responses of biological communities to changes in habitat configuration is ultimately determined by the collective responses of its constituent species and their respective life-history traits (Barbaro & Van Halder, 2009; Lees & Peres, 2008; Öckinger et al., 2010). While some life-history traits such as dispersal capacity can influence species responses in predictable ways (Cote et al., 2016), how habitat configuration influences fitness is inevitably the outcome interactions between landscape properties and multiple life-history traits for a given species. Moreover, life-history traits can respond differently to landscape properties; trade-offs may be expected where one trait responds positively, and another responds negatively to a landscape feature (Hanski et al., 2006). Consequently, there is a need for more empirical mechanistic studies evaluating how life-history traits - and particularly trade-offs among these traits - are shaped by landscape properties to understand how habitat heterogeneity and fragmentation affect species and ultimately biological communities. An enhanced focus on responses by individual species to landscape patterns may reveal mechanisms that contribute to greater understanding of community-level responses (Jones & Tingley, 2021).

The spotted owl (*Strix occidentalis*) is an exemplar of the conundrum posed by the two conservation paradigms, and thus represents an ideal species to evaluate potential trade-offs between minimizing habitat fragmentation (e.g., retaining large patches of contiguous habitat) versus promoting habitat heterogeneity (e.g., managing for juxtaposition of multiple habitat types). This species – which is at the center of management planning in many western forests – typically nests and roosts in larger patches of mature forests and some studies have found that fitness components and territory occupancy benefit from extensive areas of closed canopy and mature forests (Jones et al., 2018; Tempel et al., 2014, 2016). Moreover, the Humboldt flying squirrel (*Glaucomys oregonsis*), a primary prey species for many spotted owl populations (Munton et al., 2002), is often associated with dense canopy cover in mature forests (Meyer et al., 2005; Smith & Person, 2007). However, in some parts of their range spotted owls also forage in landscapes characterized by a mix of mature, young, and open forests (Atuo et al. 2019, Gallagher et al., 2019; Irwin et al., 2007; Waters & Zabel, 1995; Williams et al., 2011). Notably, woodrats (*Neotoma* spp.), on average are more energetically profitable than flying squirrels (1205 kJ versus 592 kJ; Weathers et al., 2001), can achieve higher densities in open/younger forests, and may be particularly accessible to owls along the edges of mature and open/younger forests where the combination of prevalent perching structures and dense prey create favorable hunting conditions (Sakai & Noon, 1997). Both the consumption of woodrats and heterogeneous habitat conditions, involving a mix forest types believed to promote to woodrat populations, have been shown to benefit spotted owl territory occupancy rates in some studies (Franklin et al., 2000; Hobart, et al., 2019a; Hobart et al., 2019b). Nevertheless, the dispersion of more suitable mature foraging habitat created by the juxtaposition of this forest type with open forest and younger forests could increase the energetic costs of foraging for spotted owls. To date, studies linking spotted owl population metrics, habitat, and prey conditions are typically coarse in scale and correlational – with no mechanistic, integrative assessments of the behavioral, trophic fitness consequences of the potential trade-offs between fragmentation and heterogeneity.

Here, we tested the hypothesis that the energetic benefits to the California spotted owl (*S. o. occidentalis)* (henceforth spotted owl) of capturing larger prey (such as woodrats) outweighs the energetic costs of greater nocturnal movement and travel distances when their mature and medium forest foraging habitat is patchily distributed or intermixed with open forest and younger forest within their home ranges. Under this hypothesis, we predicted (prediction 1) that spotted owls would travel further distances traveling to foraging sites when mature and medium forest was patchily distributed within their home ranges. We also predicted (prediction 2) that spotted owls would deliver prey items and biomass at a faster rate to nests when their home ranges encompassed greater forest heterogeneity and edge. Finally, we predicted (prediction 3) that spotted owl reproductive success would be uncorrelated, or potentially positively correlated, with the degree forest heterogeneity and edge in home ranges as a consequence of these trade-offs. Understanding these trade-offs and the potential effects of habitat composition and configuration on California spotted owls is particularly important given (i) much of their habitat occurs in mixed-ownership landscapes experiencing commercial timber harvesting, and (ii) forest managers are attempting to promote more heterogeneous forest condition to create more resilient landscapes and reduce large severe wildfires in a region experiencing unprecedented change (Jones et al., 2020).

2 Materials And Methods

2.1 | Study system

Our study took place in the northern and central Sierra Nevada, California (Fig. 1). Field work was conducted in a mix of private and public land to characterize spotted owl space use, trophic ecology, and fitness consequences across a gradient of forest conditions, particularly variation in the composition and configuration of forested stands of different ages. Specifically, we studied spotted owls in and adjacent to (1) the Eldorado Demography Study Area (EDSA; all predictions); (2) Sierra Pacific Industries' (SPI) Stirling Study Area (SSA; all predictions), and (3) with SPI's five Watershed Study Areas (WSAs; prediction three only) – areas that have been described in detail elsewhere (Hobart et al., 2019b). Briefly, these areas were characterized by mixed coniferous forests containing both patches of mature forest with overstories dominated by large trees and forests where large-tree removal has produced relatively homogenous stands dominated by medium trees. These forests typically contained high densities of trees resulting from over a century of fire suppression (Parsons & Debenedetti, 1979). Intermixed were other forest types including patches of open/brushy and younger naturally regenerating forests and plantations resulting from timber harvesting primarily on private land and wildfire, creating a mosaic of patch types across the landscape. The vegetation was typical of Sierran mixed-conifer forest dominated by Douglas fir (*Pseudotsuga menziesii*), white fir (*Abies concolor*), incense cedar (*Calocedrus decurens*), ponderosa pine (*Pinus pondersa*), sugar pine (*Pinus lambertiana*), and California black oak (*Quercus kelloggii*). Tanoak (*Lithocarpus densiflorus*) formed a dense understory in some areas.

2.2 | Owl surveys

We surveyed for owls from March 15 to August 31, 2013–2020 on both study areas. EDSA territory locations were identified as part of our long-term monitoring studies (Roberts et al., 2017; Tempel et al., 2016). Owls were located during call-based surveys at night and found during dusk/dawn surveys the following day to determine their reproductive status and roost and nesting locations (Franklin et al., 1996). Owls were fed live mice during follow-up surveys to determine nesting status and number of juveniles fledged (Franklin et al., 1996).

2.3 | GPS tagging

Based on owls found as part of the aforementioned surveys, we captured 31 spotted owls (24 males and 7 females) in 2019 and 2020 for GPS tagging using noose poles, pan raps and "hand capture" methods (Wood et al., 2021). Owls were selected opportunistically for tagging based on the accessibility of the nest for video-monitoring (see below) and the likelihood of recapture to remove transmitters. We affixed GPS tags (Alle-300, Ecotone, Poland, 10 g) to 15 of these owls weighing as tail mounts following methods in previous research (Kramer et al., 2021). We affixed a different model (Vesper 3.2 tag manufactured by ASD, Haifa, Israel; 11.6 g) to the remaining 16 individuals also as tail mounts. The second set of tags also collected vocalization data as part of another study (Reid et al., *In Review*). We programmed tags to collect locations at two-minute intervals to characterize spotted owl nocturnal movements during the nestling period in May and early June. Following the final deployment, we attempted to recapture all owls to remove GPS tags but two individuals that were not recaptured were expected to molt during that season or the following thus shedding the GPS tag.

2.4 | Nest video monitoring

We monitored prey deliveries using infrared (IR) video cameras placed at the nest sites of 15 GPS-tagged males concurrent with the collection of GPS locations. To do so, we climbed a nearby adjacent tree (10-50m from the nest tree) using a single rope technique and secured a video camera across from the nest tree. We monitored nests using AXIS Q1786 – LE 4 megapixel outdoor infrared video cameras that continuously recorded high quality images throughout the nocturnal foraging period (2000 to 0630 Pacific Daylight Time). We reviewed all video data to detect and identify prey delivered to each nest.

2.6 | Characterizing habitat composition and configuration

To understand the effects on spotted owl movements, prey deliveries, and reproductive output, we characterized vegetation conditions within individual GPS-tagged spotted owl home ranges, where the home range was estimated as the 95% KDE of the GPS points (Blakey et al., 2019). Specifically, we characterized the landscape into measures of both habitat composition (forest stand type) and configuration (spatial arrangement of forest stand types).

We classified habitat composition in a way that maintained consistency and comparability with previous work on owl-prey relationships (Hobart et al., 2019b). Thus, our classification was based on 30 m resolution gradient nearest neighbor (GNN) data, which interpolates information from an extensive forest-inventory plot network across the landscape and Landsat imagery (Ohmann & Gregory, 2002). Given that owl data spanned 2013–2020, we used GNN data from an intermediate date of 2017. However, we did not consider owl data from territories that experienced substantial vegetation change from the large and severe 2014 King Fire wildfire prior to the fire (i.e., in the breeding seasons of 2013 and 2014) to ensure no substantial mismatches occurred between mapped vegetations conditions and owl data (see analysis of reproductive output below). While timber harvesting did occur in some territories, temporal changes in habitat composition based on remotely-sensed data are very small (on average < 1% of territories) relative to the degree of spatial variation in habitat composition among territories (Table 1; Tempel et al. 2016, Jones et al. 2018) – and our analyses were focused on variation in owl behavior, diet, and reproduction that occurred among territories. Canopy cover and quadratic mean diameter thresholds used to define vegetation classes matched those of previous work (e.g. Hobart et al., 2019b). Specifically, we defined open forest as those where canopy cover was less than 40%, and divided other forested areas with a canopy cover of 40% or greater into several classes based on tree sizes: i) mature forest, when the quadratic mean diameter (QMD) of dominant and codominant trees was at least 60 cm, ii) medium forest, when QMD was between 30 and 60 cm, and iii) young forest, when QMD was less than 30 cm. Finally, we calculated the proportional area of each habitat class within each home range (Table 1).

Table 1

Metrics used to characterize habitat composition and configuration within individual spotted owl home ranges. Habitat composition metrics were derived from 30 m resolution 2017 Gradient Nearest Neighbor (GNN) data (Ohmann and Gregory (2002)) and habitat configuration metrics were calculated using 10 m 2017 California Forest Observatory data (CFO; California Forest Observatory (2020)). QMD = quadratic mean diameter. SD = standard deviation.

Metric	**Data Source**	**Definition**	**Mean (SD)**	**Min-Max**
Mature forest	GNN	Proportion of home range with forests with QMD ≥ 60 cm and canopy cover ≥ 40%	0.09 (0.08)	0.00-0.43
Medium forest	GNN	Proportion of home range with forests with QMD 30–60 cm and canopy cover ≥ 40%	0.55 (0.16)	0.08–0.90
Young forest	GNN	Proportion of home range with forests with QMD < 30 cm and canopy cover < 40%	0.19 (0.10)	0.02–0.74
Open forest	GNN	Proportion of home range with forests with < 40%	0.14 (0.15)	0.00-0.78
Medium/mature patch distance*	CFO	Mean distance to nearest neighboring patch, for each medium/mature core forest patch (height > 20 m). To delineate each medium/mature core forest patch i) identify all areas of medium/mature forest, ii) remove all area within 50 meters of young or open forest patches (of > $3600m^2$), and iii) delineate patches using the 4-neighbor rule, and removing patches < = $3600m^2$	71.8 (40.3)	2-141
Woodrat-prevalent edge	CFO	Relative woodrat-prevalent edge area in each territory where edge is defined as the area between forests with 2–10 m canopy height and > 20 m canopy height (classified using a 90 m moving window across 10 m CFO-generated canopy height)	0.013 (0.010)	0-0.058
Forest heterogeneity	CFO	Canopy texture (SD of SD, using a 90 m moving window across 10 m CFO-generated canopy height)	0.80 (0.19)	0.23–1.29

*Some territories lacked medium/mature patches, which prevented computation of this variable because patch distance was greater than home range size. In these cases, we estimated patch distance as the maximum observed value plus one standard deviation.

We characterized the spatial configuration of the landscape using finer-scale California Forest Observatory data (CFO; California Forest Observatory (2020)) describing vegetation height and canopy cover at 10 m resolution. Because fine-scale habitat configuration may be driving prey abundance and ease of capture, we used a dataset that accurately described forest structure at a finer scale from which to derive our estimates of spatial configuration. CFO is a recently developed product that uses airborne LiDAR to build models that interpolate forest structure from satellite imagery (California Forest Observatory (2020)). Tree height predictions are, on average, within 2 m of truth, and canopy cover estimates are within 7%, indicating high accuracy of predictions (Salo Sciences Inc., 2020). We used 2017

CFO estimates of canopy height and cover to estimate i) the distance between patches of medium and mature forest, ii) relative amount of edge where woodrats would likely be prevalent, and iii) habitat heterogeneity. To calculate inter-patch distance, we first defined core patch area as patches (defined using the four-neighbor rule; Turner & Gardner 2015) of at least 3600 m^2 in area where canopy height was over 20 m and which were located at least 50 m from shorter forest patches (at least 3600 m^2 in area and with canopy height at or below 20 m; see Fig. 2). We then calculated the average distance between these patches within each home range. We approximated woodrat-prevalent edge as areas where shorter vegetation (small trees and brushy areas that we presumed to be woodrat source habitat) was in close proximity to tall vegetation (where woodrats may have been less abundant but easier to capture by owls because of more perching locations for owls and less cover for woodrats). We calculated this metric using a 90 m moving window to identify all pixels where at least 30% of pixels within the moving window were between 2 and 10 m in height and at least 30% of the remaining pixels were over 20 m in height (see Fig. 2). Finally, we estimated habitat heterogeneity using the texture of vegetation height via standard deviation. We first calculated the standard deviation of canopy height within a 90 m moving window. In heterogeneous forests composed of a patchwork of clear cuts and older forest, this produced a raster with both very high values (on clear cut edges) and very low values (within clear cuts or in even-aged stands), whereas in homogeneous forests that were more contiguous, values were mostly intermediate. While this delineation differentiated between these landscapes visually, a summary statistic could not capture this pattern. Thus, we measured the standard deviation of the standard deviation raster using another 90 m moving window. As shown in Fig. 2, this clearly resulted in values that were higher in heterogeneous areas and lower in more homogeneous forests.

2.7 | Estimating distance travelled

We used the sequential GPS locations to estimate the total nocturnal flight distance each night for each individual owl. Because energetic cost is strongly correlated to distance traveled, we considered this estimate likely to be a reasonable proxy for nightly energy expenditure (Shepard et al., 2013). To account for GPS error (45 m and 23 m median spatial error for the Ecotone and Vesper tags, respectively; Kramer and Whitmore, *unpublished data*) we removed any point that was farther from both the previous and subsequent points than the distance between the previous and subsequent points, a process that removed 10% of the GPS points. We then smoothed the line using a polynomial approximation with exponential kernel algorithm to better approximate the actual distance flown by each owl each night. Finally, we calculated the mean nightly distanced travelled for each tagged individual for analyses of movements in relation to habitat conditions, as described in more detail below.

2.8 | Estimating prey and biomass delivery rates

For each nest monitored with video recorders, we estimated both prey delivery rates (number of prey items delivered per hour) and biomass delivery rates (grams delivered per hour) based on prey deliveries identified from the nest video data. Calculating prey biomass delivery rates required that we estimate the body mass of each prey item delivered. For the largest and most common prey, dusky-footed woodrats and Humboldt flying squirrels, we assumed that the mean body mass of individuals delivered to nests were equal to the body mass of individuals consumed by spotted owls as ascertained from regurgitated pellets that we collected as a part of previous studies in these areas. To calculate the mean body mass of these two species in owl pellets, we collected at least one and up to six skull and mandible measurements (depending on the condition of the prey remains) from 26 flying squirrel and 31 dusky-footed woodrat skulls or skull fragments (Table S1). We then collected the same measurements from museum specimens for which body mass estimates were available. Specifically, we visited the University of Washington's Burke Museum for flying squirrels (*n* = 86) and the University of California, Berkeley's Museum of Vertebrate Zoology for woodrats (*n* = 50). For these museum specimens, we developed predictive relationships between body mass and skull and mandible measurements using a set of univariate linear regressions of body mass against the skeletal measurements. We did not use a multiple regression approach as measurements could not be taken on all skull and mandible parts for all museum specimens or pellet samples. We then estimated body mass for remains within pellets based on the predictive relationships and measurements of skull and mandible parts in museum specimens (Table S1). For each of the two species, we then averaged body mass estimates from each prediction to determine an average mass. Using this approach, we estimated that the mean body mass of woodrats and flying squirrels consumed by spotted owls was 187.4 g (range: 110.9 to 271.2 g) and 98.8 g (range: 80.2 to 117.2 g), respectively. We estimated the mass of the secondary and generally smaller species delivered to nests according to the midpoint of body mass ranges for species presented in the literature (Reid, 2006). For example, if an owl delivered a mouse (body mass range: 15–25 g) to their nest, the assigned body mass would be 20 g. When we were unable to identify the species delivered, we assigned the body mass based on the observed size class (large, medium, small, or extra small). Thus, in the small class that included mice (15–25 g), montane voles (30–80 g), and passerines (20–120 g), the prey mass estimate was 47.5 g. We also had instances where we were able to identify that there was indeed a prey delivery but were unable to estimate the size of the prey item due to the view being obstructed by the owl or an object in frame. In these cases, we used the mean body mass of all other prey deliveries at that territory.

2.9 | Estimating reproductive output

Using reproductive histories determined as part of the spotted owl surveys conducted from 2013 to 2020 described above, we related reproductive success to the metrics of vegetation composition and configuration in Table 1. This analysis included the same 151 spotted owl territories used in Hobart et al., (2019b) but over a longer time period (Fig. 1). We treated the number of juveniles fledged (0, 1, 2, or 3) as the response variable where territorial pairs that did not attempt to nest were excluded such that 0 young fledged in this case represented the outcome of failed nesting attempts. Our rationale for this approach was that analyses of prey delivery rates to nests (i.e., prediction 2) were, by definition, constrained to pairs that attempted to nest and our objective was, collectively, to understand how the habitat-mediated variation in prey deliveries influenced the number of young fledged.

As we lacked GPS tagging data for spotted owls within all of 151 territories considered in reproductive analyses, we calculated measures of vegetation composition and configuration within circular areas approximating the size and location of owl territories. To do so, we calculated the geometric center for each territory based on the geometric mean of nest and roost locations over the study period following Hobart et al., (2019b). We then calculated the ½ nearest-neighbor distance for each territory to create a radius centered on the territory's activity center (1.12 km). We then calculated the seven metrics of habitat composition and configuration (Table 1) using methods described in section 2.6 and 2017 CFO and GNN vegetation data. Thus, as discussed above we assumed that most of variation in forest conditions was spatial rather than temporal (Tempel et al., 2016) - except for sites that experienced significant substantial modification (> 50% of area burned severely) from the King Fire during the study, in which case did not consider pre-fire reproductive data (2013 or 2014) to ensure vegetation measurements matched reproductive data temporally (n = 1).

2.10 | Statistical analyses

We used generalized linear models (GLMs) and generalized linear mixed-effects models (GLMMs) to evaluate our three predictions in program R with the packages 'glmulti' version 1.0.8 (Calcagno & de Mazancourt, 2010) and 'lme4' version 1.1–27 (Bates et al., 2015). We selected the most parsimonious model for each prediction using an all-subsets approach in which all combinations of covariates in Table 1 were evaluated as competing models, but we restricted interactions among variables (main effects only). All covariates were z-standardized to improve model fitting routines and interpretation (Schielzeth, 2010). We selected models using the Akaike information criterion with sample size correction (AICc) and models within 2 AICc were considered competitive (Burnham & Anderson, 2002). Models containing pairs of variables with correlation coefficients greater than 0.70 were not considered. We report the 85% confidence interval for model coefficients because this interval is more compatible with AIC approaches than a 95% confidence interval (Arnold, 2010). We estimated a pseudo-R^2 for GLMs and GLMMs using a corrected likelihood ratio-based approach (Nagelkerke, 1991) with the R package 'rsq' version 2.2 (Zhang, 2021). All-subsets selection as conducted using package 'glmulti' for GLMs and the 'dredge' function in the package 'MuMIn' version 1.43.17 (Barton, 2020) for GLMMs. For each prediction, we selected the distributional family *a priori* before model fitting and selection. All models were fitted using maximum likelihood estimation.

For prediction 1 (distance traveled; *n* = 31), we specified a Gamma distribution with a log link. For the sake of parsimony, prior to considering the habitat covariates in Table 1, we first modeled "nuisance" effects that included sex, reproductive status, and tag type (because of differences in locational precision) as categorical fixed effects; the model contained no random effects. We then included supported from this modeling stage in all models incorporating habitat covariates in a second modeling stage. For prediction 2 (prey biomass and prey item delivery rates; *n* = 15) we specified a Gamma distribution with a log link. Similar to prediction 1, this model contained only fixed effects. For prediction 3 (reproductive output), we specified a Gaussian distribution. Number of young fledged follows a positive discrete distribution ranging from 0 to 3. Although the data distribution for young fledged is not Gaussian, applying normal regression procedures (or a GLM procedure with Gaussian error) is less biased than GLM alternatives that follow positive discrete error distributions, such as Poisson (McDonald & White, 2010). Territories were repeatedly visited across eight years, so we treated ‘territory’ as a random effect. Reproductive output can also vary substantially among years in spotted owls (Franklin et al., 2004), so we treated ‘year’ as a random effect.

3 Results

3.1 | Distance travelled

We acquired 33,056 usable nocturnal locations from the 15 spotted owls tagged with Ecotone GPS units after culling locations taken below 3.7 voltage that typically have greater positional error (S. Whitmore *unpublished data*). We acquired an additional 45,460 usable nocturnal GPS locations from the 16 spotted owls tagged with Vesper GPS units after culling locations with horizontal dilution of precision (HDOP) < 10 and satellites < 6. We also deleted any partial nights from the estimates of distance travelled for both GPS tags. Thus, for analyses purposes, we collected a mean 1,466 (range: 553-4,327) locations per owl over a mean of 5.3 nights (range: 2–15). Mean 95% KDE size for these 31 individuals was 400 ha (SD = 377).

Our “nuisance” analysis suggested that nightly distance travelled differed as a function of breeding status and tag types, but not sex or month – and we therefore carried over the former two effects into the second stage of modelling that included habitat covariates. Based on the Spotted owls travelled shorter distances when there was more medium forest available within their territory ($\beta_{\text{medium forest}}$ = − 0.23, 85% CI = [− 0.23, − 0.05]) based on the top model following all-subsets selection in the second stage (AICc = 115.88; pseudo-R^2 = 0.87; Table 2). Breeding owls traveled farther distances than non-breeders (breeders mean nightly distance = 7,375 m and non-breeders mean nightly distance = 3,648; Fig. 3).

Table 2

Most supported generalized linear models from each of three predictions. AICc = Akaike information criterion; ΔAIC = difference between AIC and the top model in the set; *w* = Akaike weight; K = number of parameters. Depending on the degree of model selection uncertainty, we display models within 2 (denoted with *) or 5 AICc of the top model. Intercept-only (null) models were included in each set. K for Prediction 3 includes two random effects (year and territory).

Model	**AICc**	**ΔAIC**	***w***	**K**
Prediction 1				
"Nuisance" analysis for distance traveled				
breeding + tag type	122.07	0.00	0.433	3
breeding + tag type + nights	123.46	1.38	0.217	4
sex + breeding + tag type	124.89	2.81	0.106	4
breeding + tag type + month tag deployed	124.91	2.83	0.105	4
sex + breeding + tag type + nights	126.20	4.12	0.055	5
breeding + tag type + nights + month tag deployed	126.45	4.37	0.049	5
Distance traveled				
breeding + medium forest + tag	115.88	0.00	0.247	4
breeding + medium forest + mature + tag type	118.52	2.64	0.066	5
breeding + medium forest + young forest + tag type	118.55	2.66	0.065	5
breeding + medium forest + woodrat prevalent edge + tag type	118.56	2.67	0.065	5
breeding + medium forest + medium/mature patch distance + tag type	118.73	2.85	0.059	5
breeding + open forest + medium forest + tag type	118.94	3.06	0.053	5
breeding + medium forest + heterogeneity + tag type	118.95	3.07	0.053	5
Prediction 2				
Prey biomass with potential influential territory				
heterogeneity	131.85	0.00	0.194	2
intercept-only	132.84	0.98	0.118	1
mature forest	133.93	2.07	0.069	2
woodrat prevalent edge	134.46	2.60	0.053	2
young forest	134.55	2.69	0.050	2
Prey biomass without potential influential territory				

Model	AICc	ΔAIC	*w*	K
open forest + woodrat prevalent edge	107.66	0.00	0.167	3
open forest	108.25	0.58	0.125	3
open forest + woodrat prevalent edge + medium/mature patch distance	108.46	0.79	0.112	4
open forest + medium/mature patch distance	109.67	2.00	0.061	3
intercept-only	110.01	2.34	0.052	1
Prey delivery rate				
intercept-only	-11.07	0.00	0.190	1
heterogeneity	-10.34	0.73	0.131	2
woodrat prevalent edge	-9.54	1.53	0.088	2
mature forest	-8.68	2.39	0.057	2
young forest	-8.56	2.51	0.054	2
Prediction 3				
*Reproductive success**				
mature forest + open forest + mature forest * open forest	543.2	0	0.135	6
mature forest + open forest	543.4	0.14	0.126	5
mature forest	543.8	0.6	0.100	4
medium forest + young forest	544.7	1.47	0.065	5
Woodrat prevalent edge + mature forest + open forest	544.8	1.59	0.061	6

3.2 | Prey biomass and prey delivery rates

Based on the video data, we observed 358 potential prey deliveries by spotted owls to their nests. Of these, 62.6% were identified to species, 18.7% were identified according to size, 6.4% were of unknown species and size, and it was uncertain whether a prey was delivered in 12.3% of cases. We identified eight different species delivered to nests, of which dusky-footed woodrats and Humboldt flying squirrels were the most common (41.5 and 40.2%, respectively). The less common species were bats (*Myotis spp.*, 0.4%), mice (*Permoyscus spp.*, 13.8%), montane voles (*Microtus montanus*, 1.8%), Townsend's moles (*Scapanus townsendii*, 0.9%), pocket gophers (*Thomomys spp.*, 0.9%) and passerines (*Passeriformes* (order), 0.4%).

Spotted owls delivered prey biomass at a faster rate to nests when their territories contained more heterogeneous forest conditions ($\beta_{\text{habitat heterogeneity}}$ = 0.22 [0.05, 0.41]); based on the top model – and only model (AICc = 131.9; pseudo-R^2 = 0.24; Fig. 4A) to outperform the null (AICc = 132.8). However, this relationship may have been influenced by a single observation with a high rate of biomass delivery (117 g per hour) at a nest for which we only collected 10.5 hours of data before the juveniles fledged and for which a relatively high proportion of prey were not identified to species. Accordingly, we repeated the model selection procedure after removing this data point. The top model from this second analysis (AICc = 107.7; pseudo-R^2 = 0.50) suggested that spotted owls delivered prey biomass at a slower rate when there was a higher proportion of open forest within their home range (β_{open} = – 0.16, 85% CI = [– 0.26, – 0.07]; Fig. 4C) and at a higher rate to nests when more woodrat-prevalent edge occurred within their home range ($\beta_{\text{woodrat–prevalent edge}}$ = 0.12, 85% CI = [0.04, 0.21]; Fig. 4B). For prey delivery rate, the null model (AICc = – 11.08) outperformed all other models indicating that delivery rates by spotted owls were unrelated to the measures of vegetation composition and configuration we considered (Table 2).

3.3 | Reproductive output

Reproductive output was lower for owls with more mature forest ($\beta_{\text{mature forest}}$ = – 0.11, 85% CI = [– 0.19, – 0.04]) and open forest (β_{open} = – 0.17, 85% CI = [– 0.33, – 0.02]) based on the most supported model (AICc = 543.4; Table 2). However, given that heterogeneity in vegetation conditions increased biomass delivery rates to nests (prediction 2), we also examined a post-hoc model to explore a potential interaction between mature and open forest. This *post hoc* model (AICc = 543.2) was slightly more supported than the additive model and indicated that the effect of mature forest on reproductive output was conditional on the amount of open forest in a territory ($\beta_{\text{mature forest*open}}$ = 0.27, 85% CI = [0.01, 0.54]. Specifically, the benefits of mature forest on reproductive output were only realized when territories also had a high proportion of open forest (Fig. 5). Collectively, open forest, mature forest, and their interaction explained 33% of the variance in reproductive output among territories following the variance components approach of Franklin et al. (2000).

4 Discussion

Improved understanding of the mechanisms by which species respond behaviorally and demographically to environmental heterogeneity and fragmentation is needed to mitigate the potential effects of land use change and develop informed conservation plans. Here, we demonstrate that the effects of habitat configuration on a species considered to be a barometer of mature forest conditions are complex, where (i) the prevalence of medium forest reduced nocturnal movements, (ii) edges between taller and shorter forests increased rates of biomass delivered to nests; and (iii) a mixture of mature and open forest increased reproductive output. Thus, it seems that medium forests may help reduce energy expenditures during nocturnal activities that include foraging, but a mixture of forest types provide the greatest benefit prey acquisition and ultimately fitness (as measured by reproductive output). These findings are broadly consistent with previous studies demonstrating that heterogenous forest conditions can, in some circumstances, benefit spotted owl fitness by increase the abundance or availability of prey (Franklin et al., 2000; Hobart et al., 2019a). Yet, we provide, for the first time, mechanistic and integrative explanation of how habitat configuration benefits spotted owls by shaping their movement patterns, prey capture success, and fitness. More broadly, our study highlights that the line between habitat fragmentation and heterogeneity can be a blurry one and depends on species-specific traits as they relate to patch and landscape properties.

Spotted owls made shorter nightly movements when there was more medium forest available within their home range, which presumably resulted in lower energetic expenditures, and, conversely, travelled longer distances when this forest type was less available. While movement distances were not associated with the medium/mature patch distance or other measures of habitat configuration we considered, the negative association between movement distance and medium forest was generally consistent with our first prediction. Medium forest was the most prevalent forest type within spotted owl home ranges, on average exceeding half of the home range area (Table 1) and home ranges containing a high fraction of this forest type seemingly reduced energy expenditures associated with locomotion in spotted owls. We suggest that high proportions of medium forest afforded more direct paths to foraging sites at more heterogenous locations (Fig. 6) – and potentially locations employed to meet other life history demands such as territorial defense (Wood et al., 2019). Indeed, our previous work suggest that successful prey capture sites, particularly for woodrats, often occur in more open canopy and heterogenous areas (Zulla et al., In Review). Further, spotted owls often select medium (and mature forests) for nocturnal activities based on GPS and VHF tagging agnostic to activity (Atuo et al., 2019; Kramer et al., 2021b). Perhaps the frequent use of this forest type in our study region reflects commuting to more high-quality foraging sites, and potentially provides concealment from predators more associated with open habitats such as great-horned owls (*Bubo virginianus*). In addition, breeding individuals had substantially greater nightly movement distances than non-breeders, almost certainly because they were more active owing to movements to deliver prey from foraging sites to nests (Zulla et al. In Review). However, breeding status and medium forest were not substantially correlated (r = -0.30), such that tests of these two effects in the most supported model should have been independent.

While medium forests reduced nocturnal movements and potentially benefited spotted owls energetically, edges between taller forests typically considered spotted owl habitat and shorter forests more likely to constitute woodrat habitat increased the rate at which adults (Fig. 4B) delivered prey to nests. On average, less than 1% of 95% KDE home ranges for the 15 tagged spotted owls included in the prey delivery analyses were affected by severe fire since 1986 and less than 4% of open forests in owl 95% KDE home ranges overlapped severe fire – collectively indicating that woodrat-prevalent edges in this study were mostly created by forest management on private lands rather than severe fire. Thus, this result supports previous stable isotope work in the Sierra Nevada demonstrating that, in some mixed-ownership landscapes, forest heterogeneity can increase woodrat consumption in adult spotted owls, which in turn increases territory occupancy rates and landscape-scale population densities (Hobart et al., 2019a). This result is also consistent with spotted owls having higher fitness in territories characterized by higher levels of forest heterogeneity (Franklin et al., 2000), although the mechanisms linking fitness and heterogeneity were not evaluated in this study. Indeed, we provide long-sought support for the hypothesis that the juxtaposition of older forests and woodrat habitat promotes hunting success in spotted owls (Sakai & Noon, 1993). The juxtaposition of these two habitats could both (i) promote the dispersal of individual woodrats from high-density populations in shorter (younger) forests into taller (more mature) forests, and (ii) allow spotted owls to capture woodrats at these ecotones (Sakai & Noon, 1997). While we also found that spotted owls delivered biomass at a faster rate to nests when our measure of habitat heterogeneity was high, we caution that this result was strongly influenced by a single nest that was only monitored for a short period of time and for which it was unclear whether prey were delivered in several instances. Thus, while it may seem reasonable that fine-scale variation in forest age (as proxied by tree heights) could promote woodrat captures, we suggest that stronger evidence exists for the importance of edges between taller (older) and shorter (younger) forests. We note the edges promoting prey deliveries were typically the result of commercial logging rather than wildfire in this particular study (e.g., Fig. 2C). Indeed, none of the four territories with large values for edge in Fig. 4C experienced any recent severe fire. Importantly, however, the rate at which spotted owls delivered prey biomass to nests declined with the proportion of open forest in their territories. While some open areas, particularly those with substantial brush cover, likely harbor dense woodrat populations, large expanses are unlikely to be sources of prey to spotted owls unless sufficient taller forest is present in the vicinity.

Spotted owl reproductive output, unexpectedly, decreased with increasing proportional areas of mature forest, as well as decreased with more open forest, based on the most supported *a priori* model. Indeed, we would have expected that, by itself, a greater proportional area of mature forest would provide better opportunities for nest site selection, concealment from predators, and protection from inclement weather conditions (Franklin et al., 2000) – particularly since this forest type constitutes a relatively small proportion of spotted owl home ranges (0.09, Table 1). However, a *post-hoc* interactive model that was slightly more supported suggested that reproductive output was relatively high when territories contained greater proportional areas of *both* mature and open forests. Thus, in the absence of a positive main effect for mature forest, we suggest that a more likely explanation for higher reproductive output for spotted owls containing a mix of mature and open forest involves enhanced foraging success – particularly in light of the benefits of edge habitat to prey deliveries to nests and presumably hunting success. Specifically, a faster rate of prey biomass delivery by adult spotted owls to nests afforded by greater edge between taller and shorter forests is likely to reduce nestling mortality and nest abandonment by breeding females. Although we acknowledge that woodrat-prevalent edge did not explain appreciable variation in reproductive output, we suggest that landscapes characterized by an interspersion of mature and open forest are likely to contain forest structural characteristics promoting the capture of woodrats but that we were unable to quantify. Further, flying squirrels can be more abundant in mature forests, such that territories containing greater amounts of both forest types may harbor a greater diversity of prey types and thus overall prey availability. Thus, while the exact mechanism behind higher reproductive output in territories containing a mix of open and mature forest is uncertain, we suggest that enhanced prey access, hunting success, and deliveries to nests in territories with a mosaic of forest stand ages – and edges between forest stands – can lead to emergent benefits to spotted owl fitness in some ecological settings. Further, even if the association between reprodtuctive output and mature and open forests were negative, as suggested by the top ranked a priori model, there was no evidence greater communting distances in territories with less medium forest (and thus presumably greater heterogeniety) incurred cost to reproductive success.

Large scale loss and fragmentation of northern spotted owl habitat from commercial timber harvesting appears to have contributed to population declines in the Pacific Northwest, where the Humboldt flying squirrel is the primary prey species (U.S. Department of Interior, 1990). However, our results indicate that enhanced foraging opportunities in landscapes containing heterogenous forest conditions – with stands 10s of ha in size – resulting in part from timber harvesting may benefit some fitness components (e.g., reproduction). Previous work in the Sierra Nevada similarly suggested owl can have higher reproduction and territory occupancy rates as well as smaller home ranges in such landscapes (Hobart et al. 2019a,b). Similarly, wildfire that create fine-scale heterogeneity seems to benefit spotted owl foraging, but larger-scale loss of forested habitat from severe fire (severely burned patches 100s of ha in size) can render habitat unsuitable for foraging (Jones et al. 2016, Kramer et al. 2021a). Thus, there likely exists a threshold in terms of habitat modification where heterogenous landscapes become fragmented by large expanses of open areas, reducing at least some fitness components and ultimately population density. However, further research beyond this study is needed to understand the nature of such thresholds with respect to the composition and configuration of forest types within, not just spotted owl home ranges, but landscape scales as well. We also acknowledge that our results likely only apply to spotted owls occurring in landscapes such as the low- to mid- elevational forests of the Sierra Nevada where woodrats can occur in high densities in younger forests and brushy open forests. Responses to changes in habitat composition and configuration are likely to differ in landscapes where flying squirrels are the primary prey of spotted owls, such as higher elevation forests (Hobart et al., 2019a). Finally, our focus was on reproductive output given the tight linkage between prey availability and breeding often observed in owls (Dawson & Bortolotti, 2000), but other fitness components - such as individual survival - can respond differently to habitat conditions (Franklin et al., 2000; Tempel et al., 2014). Thus, while further work is needed to understand linkages between habitat heterogeneity and spotted owl behavior, foraging success, and population dynamics in other forested landscapes, our study highlights new, integrative approaches (e.g., high temporal resolution GPS tags and nest video monitoring) that can yield novel insights into such questions.

More broadly, our results highlight the blurry line between habitat heterogeneity and fragmentation in practice. Typically, heterogeneity is considered “good” and fragmentation is considered “bad” for species, where landscapes can transition from heterogenous to fragmented if some threshold is exceeded as a result of some form anthropogenic change (Franklin et al., 2002). While we do not disagree with this distinction in principle, in practice, the terms heterogenous and fragmented can be difficult to apply in some landscapes. Responses to changes in the composition and configuration of habitat types vary among species and, within species, can vary among behavioral activities and fitness components. Further, a given agent of change – e.g., timber harvesting or wildfire – can lead to good heterogenous or bad fragmented conditions depending on the grain and scale of the change. Thus, studies of species of conservation concern in human-affected landscapes will benefit from integrative assessments of responses to habitat composition and configuration that evaluate multiple aspects of the species life history and trade-offs among them.

Declarations

Funding

Funding was provided by the US Forest Service Region 5, Pacific Southwest Research Station, and Sierra Pacific Industries.

Competing interests

The authors declare no conflict of interest.

Author's contributions

MZP, SCS, BPD, KNR, and JJK conceived the study; CJZ, RJG, BPD, and KNR led data collection, with contributions from KGK, WJB and SAW; CJZ, GMJ, HAK, JJK, and MZP designed the analysis; CJZ, GMJ, HAK, and MZP analysed the data; CJZ, GMJ, HAK and MZP wrote the manuscript. All authors provided critical feedback and gave final approval for publication.

Acknowledgements

We thank the many technicians who assisted in collecting the data for this project. We thank Jim Baldwin for help with statistical methods and data visualization.

Data availability

Data and R code is available from CJZ on request.

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Figures

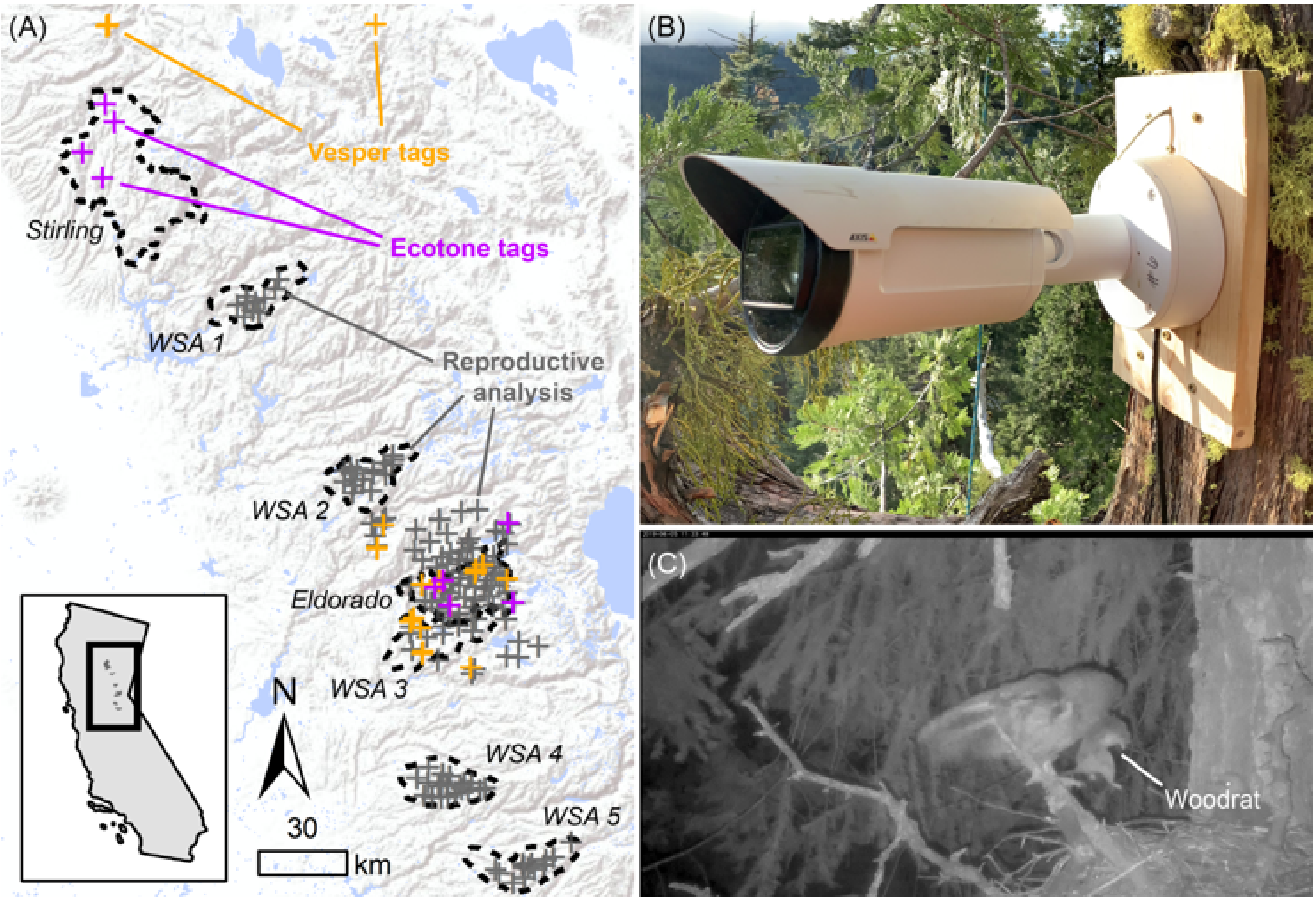

Figure 1

(A) Map of Sierra Nevada, USA depicting locations of California spotted owl territories sampled in the study. (B) Video camera adjacent to a spotted owl nest. (C) Prey delivery of dusky-footed woodrat (*Neotoma fuscipes*) recorded on the video camera.

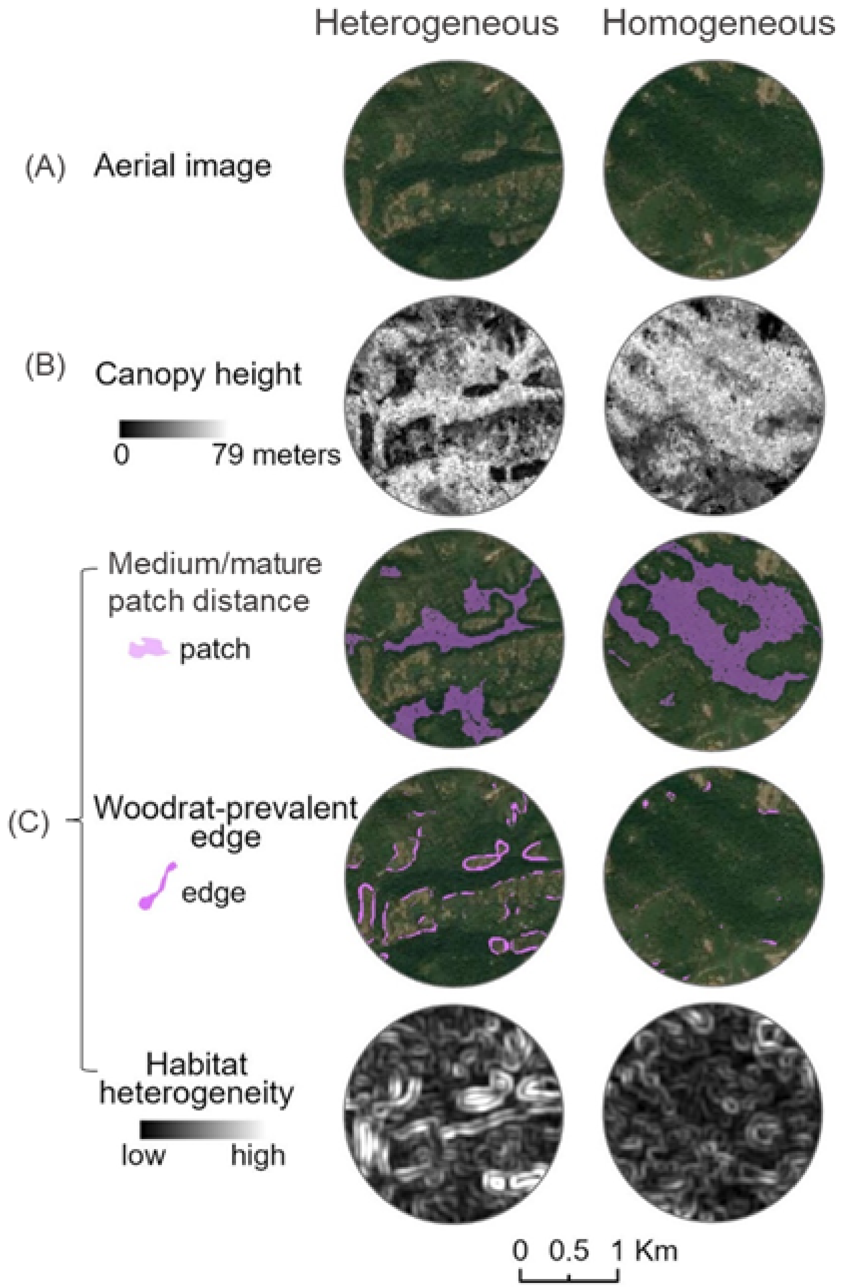

Figure 2

(A) NAIP imagery for a heterogenous and homogenous spotted owl territory. (B) Canopy heights for the same two territories based on 2017 California of Forest Observatory (CFO) data. (C) derived measures of habitat configuration for these territories calculated from CFO tree height data.

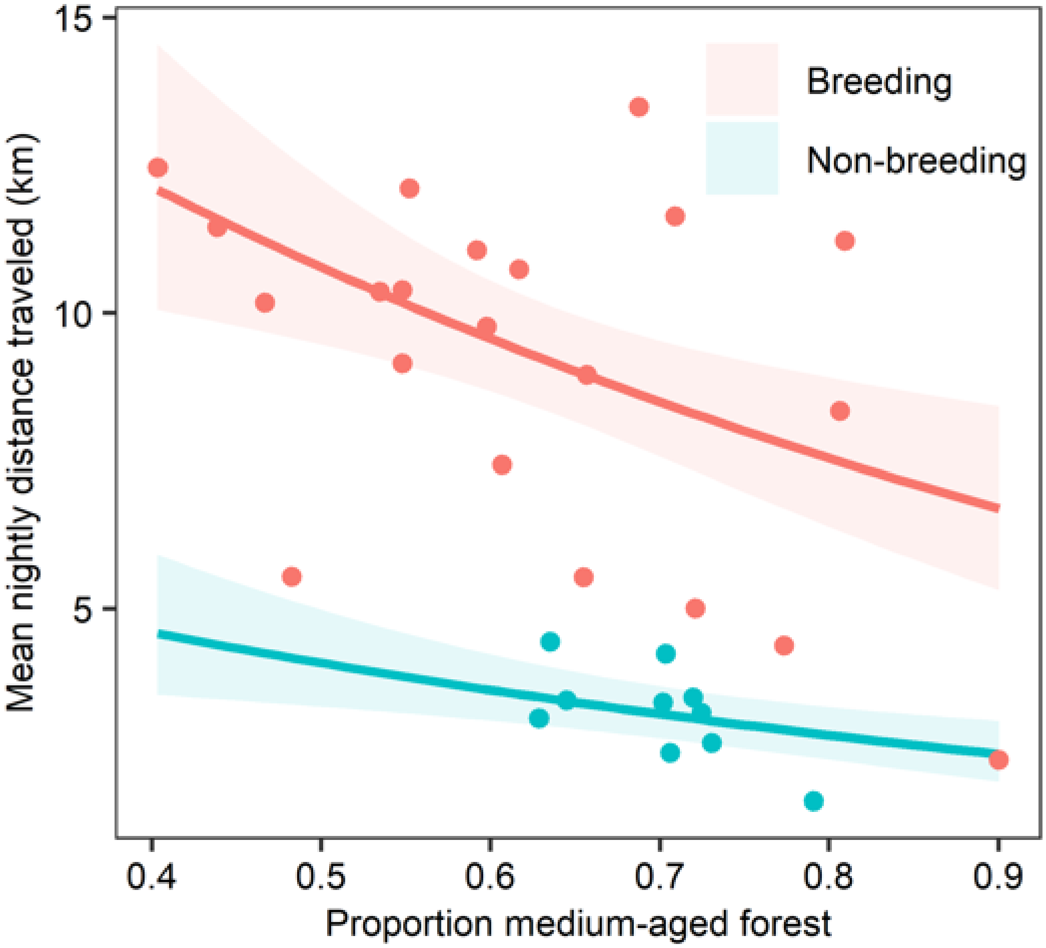

Figure 3

Mean nightly distanced moved for breeding and non-breeding owls as a function of the proportion of their home range containing medium forest

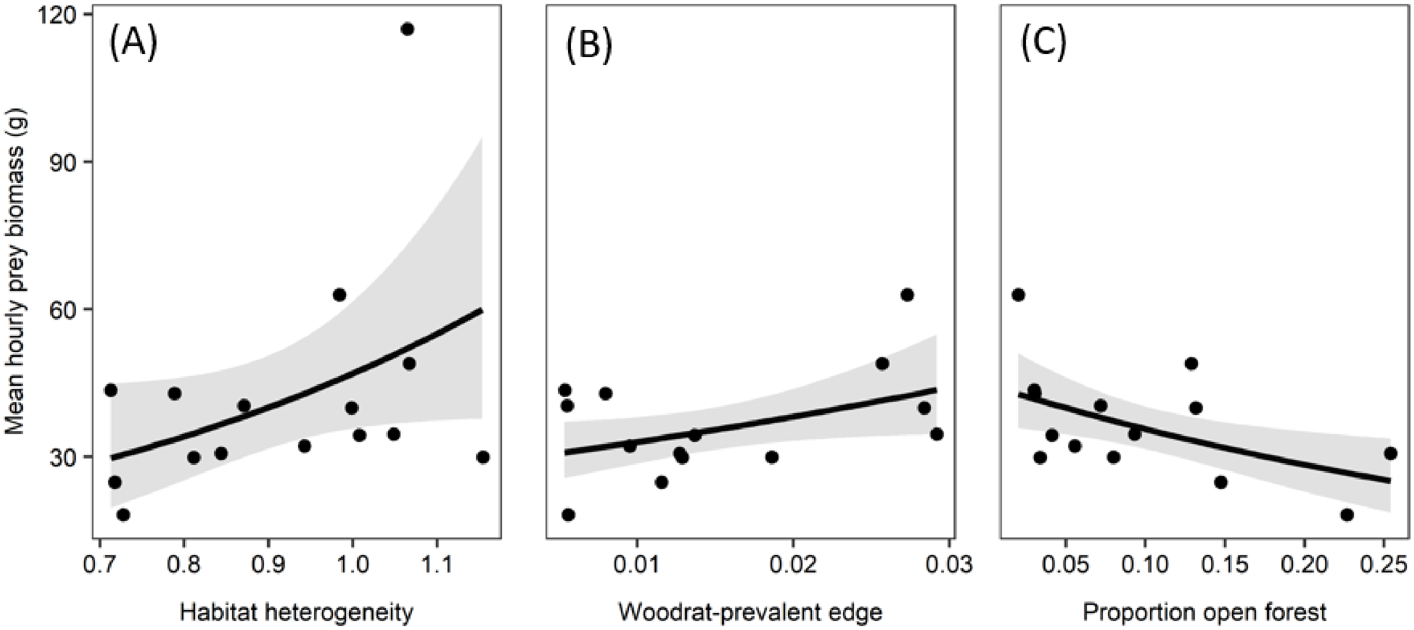

Figure 4

Effects of habitat composition and configuration on prey biomass delivery rates to nests by spotted owls in the Sierra Nevada, California.

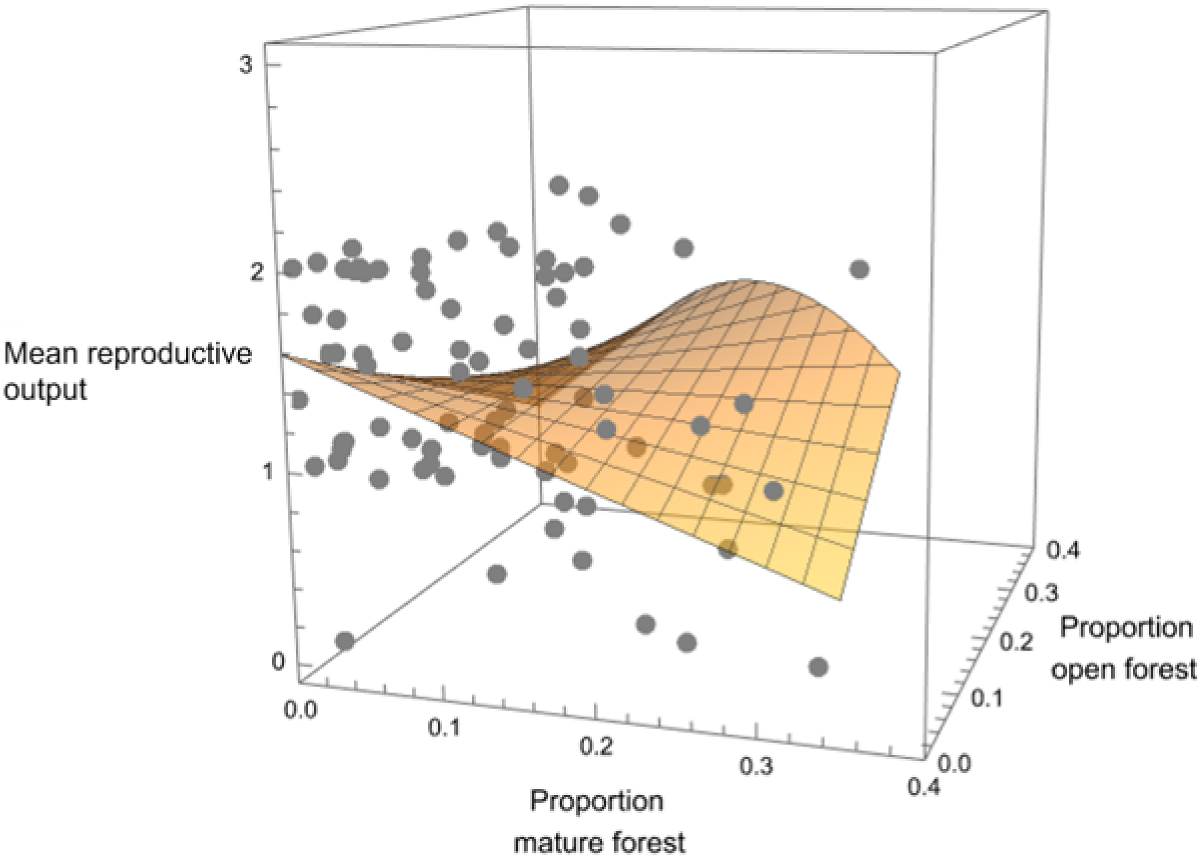

Figure 5

Mean reproductive output as a function of interacting effects of the proportion of mature and the proportion of open forest within territories for nesting spotted owls in the Sierra Nevada, California.

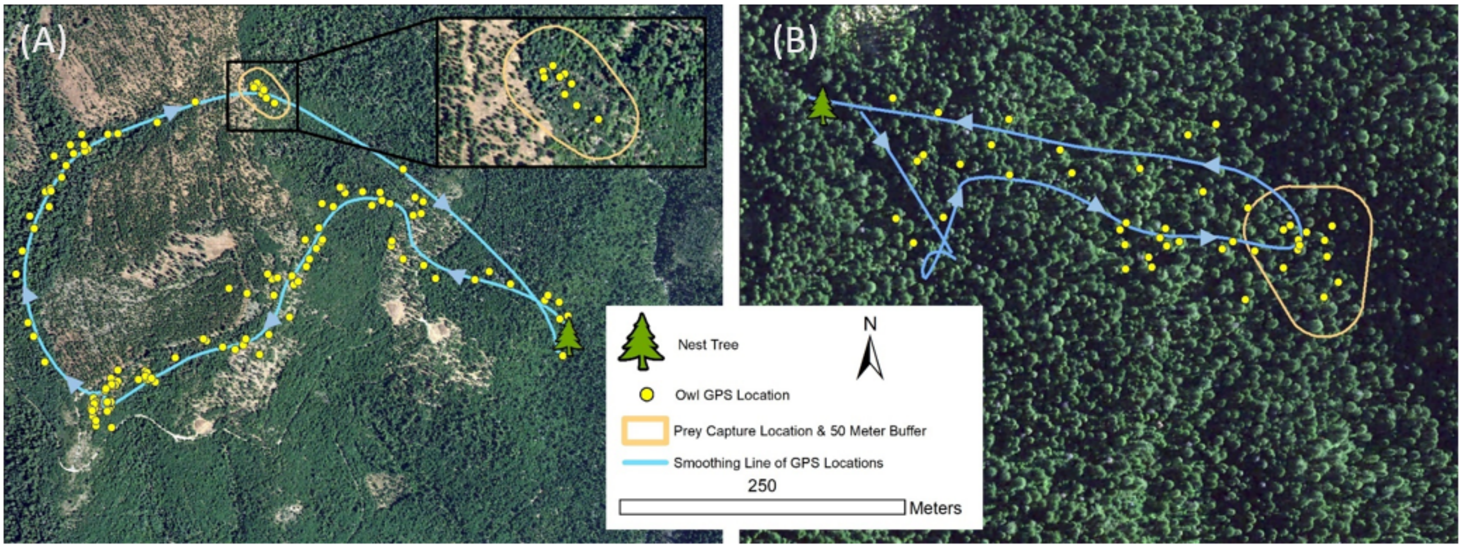

Figure 6

Two examples of spotted owl movement paths away from and back to nest sites following successful prey captures in the Sierra Nevada, California. A) a more circuitous path in areas with less medium forest and B) a more direct path in areas with more medium forests. Note the prey capture sites are shown with tan shaded polygons (see Zulla et al. In Review for methods)

Supplementary Files

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- TableS1.docx