Canada Lynx Carrying Capacity in Washington

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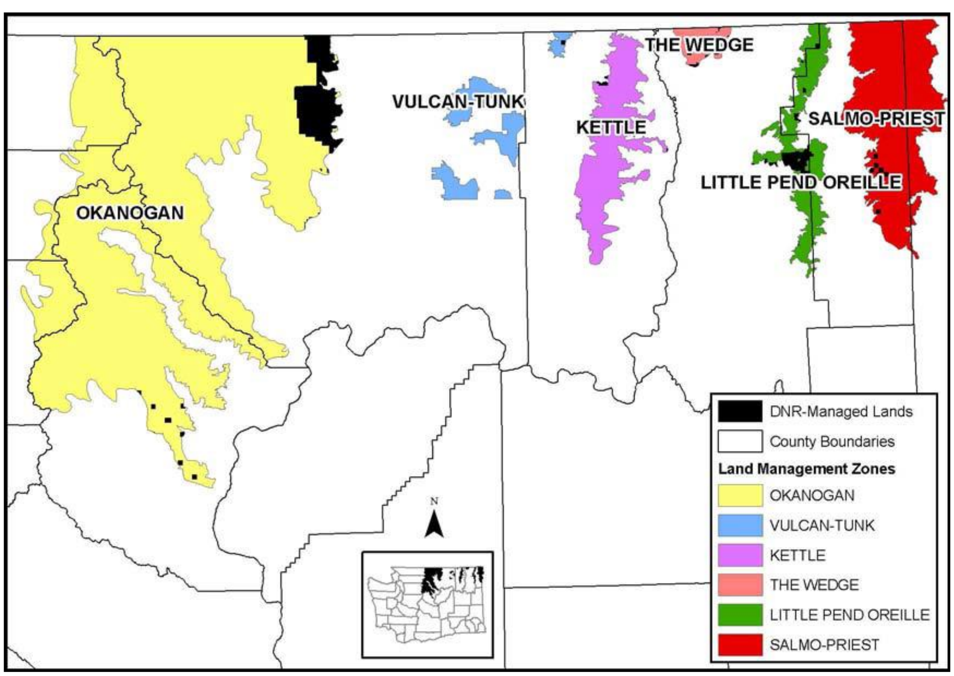
INTRODUCTION AND OBJECTIVE

Canada lynx (*Lynx canadensis*) is a species native to boreal forests of north-central and north-eastern Washington State. Once found in large numbers, particularly in the northern portion of the state, populations have declined due to habitat loss and hunting (Lewis 2016). The Canada lynx was listed as a Washington State threatened species in 1993, resulting in development of a recovery plan in 2001 (Stinson 2001). Lynx were listed as a Threatened species under the Federal Endangered Species Act in April 2000. Key threats identified in the Washington recovery plan included: forest management, fire and fire suppression, insect epidemics, and management of lynx harvest and habitats in southern British Columbia. Fifteen years later, these threats are still identified as important issues while recent research suggests climate change is likely to impact lynx, potentially exacerbating habitat loss through increased wildfire, leading to even smaller and more isolated populations in the future with decreased habitat suitability and genetic diversity (Hoving et al. 2005, Gonzalez et al. 2007, Yan et al. 2013).

Historically lynx were believed to occupy six Lynx Management Zones (LMZ), but Washington's lynx population is now largely restricted to the Okanogan LMZ (Fig. 1) (Lewis 2016), which falls under multiple land-management jurisdictions, including the Okanogan-Wenatchee National Forest, North Cascades National Park, Mount Baker-Snoqualmie National Forest, and Washington Department of Natural Resources. Occasional detections of lynx in the Kettle LMZ suggest lynx are present but likely not part of a resident population (Lewis 2016). The Kettle LMZ is predominantly managed by the Colville National Forest and the Confederated Colville Tribes.

Over the past 35 years understanding of lynx habitat use and population ecology, and methods to estimate the potential carrying capacity of wildlife populations within ecosystems have advanced tremendously. Our goal was to synthesize these advances and integrate spatial habitat data and demographic parameter estimates using a spatially explicit, individual-based population modeling approach. We used this model to address two questions: 1) What is the potential carrying capacity for Canada lynx in the Okanogan and Kettle LMZs, and 2) How have changes in habitat influenced carrying capacity over time within those LMZs?

Figure 1. Lynx management zones (LMZs) in Washington indicate the general areas historically occupied by lynx in northcentral and northeastern Washington (WDNR 2006).



ANALYSIS AREA

Our analysis area included the portion of the Okanogan LMZ north of Lake Chelan and the entire Kettle LMZ. The Okanogan LMZ is approximately 9,200 km^2 (3,552 mi^2) and the Kettle LMZ is approximately 3,300 km^2 (1,274 mi^2) (Fig 2). Both LMZs include a range of land uses from designated wilderness to multiple use resource lands to heavily populated urban areas.

The Okanogan LMZ varies from extensive lush subalpine forests and alpine meadows along the central spine of the North Cascades Mountains, transitioning rapidly to dry forests and dry, lowland valleys on the eastern portion of the ecosystem. Elevation ranges from 242 m in the eastern valleys, to peaks reaching 2755 m. Road densities vary across the landscape with a large expanse of predominantly roadless area in the western and northwestern portion of the LMZ. Similarly, the Kettle LMZ varies from subalpine forests and alpine meadows along the central spine of the Kettle Range, then transitions rapidly to dry forests and dry, lowland valleys along all edges of the LMZ. Elevation ranges from 390 m around the edges of the LMZ, to peaks exceeding 2,100 m along the center of the LMZ. Road densities vary across the landscape with minimal expanses of roadless areas.

Both LMZs share a northern border with British Columbia. The LMZs are divided into Lynx Analysis Units (LAUs) to identify assessment units for monitoring and evaluation of cumulative effects (Gaines et al. 2003, ILBT 2013). These analysis units approximate a female lynx home range and are large enough to allow the assessment of seasonal habitats and the cumulative effects of human activities on these habitats. There are 50 LAUs in the Okanogan LMZ and 14 LAUs in the Kettle LMZ (Fig 2).

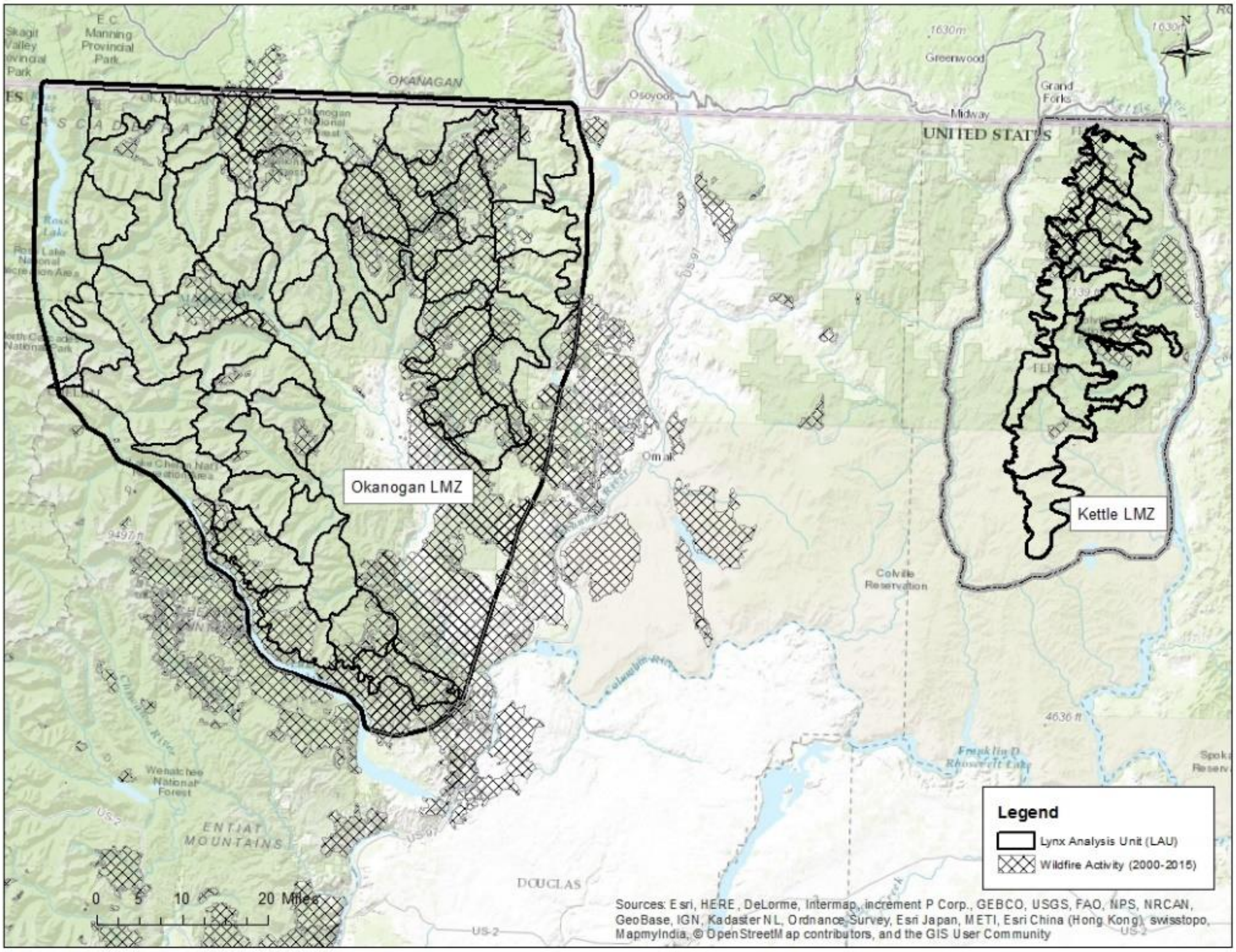
Both LMZs are also located in fire-prone landscapes with varying fire return intervals and risk for large fires (Hessburg et al. 2005, Perry et al. 2011). Over the past 15 years both of these areas have experienced an increase in substantial wildfire activity. Wildfires have impacted over 2000 km^2 within the Okanogan LMZ study area and 360km^2on the Kettle LMZ.

METHODS

To estimate carrying capacity we developed a suite of spatially-explicit, individual-based population models using HexSim software (version 4.0.3.0, Schumaker 2016) that integrated information on habitat selection, and population dynamics and changes in resource availability. HexSim software provides a framework for implementing population simulation models that has been used to investigate potential population outcomes based on empirical information regarding habitat associations and demographic rates (Heinrichs et al. 2010, Spencer et al. 2011, Huber at al. 2014). We developed Canada lynx population models that provided the appropriate information and flexibility to address two key questions: 1) What is the potential carrying capacity for lynx in the Okanogan and Kettle LMZs? and 2) How have wildfire and habitat changes influenced carrying capacity?

Application of HexSim required information on resource selection, home range size, dispersal, survival, and fecundity. We used data primarily from the Okanogan LMZ and expert knowledge from biologists familiar with lynx in Washington to populate these parameters. When site-specific data were unavailable we used information from the literature, primarily from ecosystems that resembled the southern periphery nature of the Okanogan and Kettle LMZs. We then extrapolated this model to the Kettle LMZ.

Figure 2. Okanogan and Kettle Lynx Management Zones, Lynx Analysis Units and wildfire activity from 2000 through 2015 within Washington State, US.



Development of Resource Layers – Lynx Habitat Modeling

HexSim requires that each hexagon within the model be assigned a habitat resource value based on the quality of habitat within the hexagon. To estimate carrying capacity for the two different LMZs at two time periods, we built several different resource layers based on available spatial data. This resulted in resource layers that represented:

1) OLMZ 2013 post-fire
2) OLMZ 2000 pre-fire
3) KLMZ 2015 post-fire
4) KLMZ 2000 pre-fire

To include spatial data that could show changes on the landscape we included canopy cover, forest structure and greenness in our model selection process. We anticipated that these variables would change between the pre and post-fire conditions in response to the effect of not only wildfire but also effects of harvest, insect and disease, and succession.

The initial resource values and habitat quality classifications were calculated using a resource selection function (RSF) (Manley et al. 2002, Proctor et al. 2015). We used GPS data from radio-collared lynx within the Okanogan LMZ to assess habitat selection at the scale of the Lynx Management Zone for both female and male lynx to develop a general annual model for the region. Developing an RSF model for the Okanogan LMZ based on telemetry data provided a model of "current" habitat selection. We acquired GPS data from Washington Department of Fish and Wildlife (WDFW) for 16 lynx over the time period: February 2008 through June 2013. We selected a random sample of 80% of available lynx locations for model development and withheld the remaining 20% for model evaluation.

We estimated a 100% minimum convex polygon range of all of the lynx telemetry locations to delineate our study area for model development. We only used locations within the United States, due to spatial data layer constraints. We used GPS radio-collar locations and an equal number of random locations from within the 100% MCP home range of all lynx to develop the RSF. We estimated model parameters with mixed effects logistic regression with individual lynx as a random effect (n=14) and applied a square root transformation to transform and normalize the positive skewing of exponential RSF values using R software (version 3.2.2, R Development Core Team, Vienna, Austria) and ArcGIS (version 10.4, ESRI, Inc.). Only three of the collared lynx were female so we pooled male and female lynx telemetry data to provide a more robust analysis of lynx habitat selection. We acknowledge that male selection may differ from females but the pooled information likely provides an adequate general picture of habitat selection. We tested all covariates for pairwise correlations (Spearman) and when correlations were found ($r >= 0.7$) we did not use those pairings in the same model. All continuous variables were standardized to examine relative influence on RSFs.

We developed a set of 30 *a priori* models and used Akaike's Information Criterion (AIC, Burnham and Anderson 2002) to select the model that best fit the structure of our data. We calculated a bootstrapped (n=100) mean and confidence interval for resultant coefficient estimates. Although we recognize that this set of models may be conservative, our objective was to provide a descriptive and biologically meaningful multivariate model of lynx resource selection that could be generalized to the population and provide the foundation for subsequent population carrying capacity modeling.

We examined selection ratios (use/availability) for individual lynx between the model evaluation dataset and model development dataset to assess how well the RSF predicted use. We mapped the resource selection function across the Okanogan LMZ and initially classified the transformed RSF values into 10 equal interval bins where habitat use equaled the proportion of withheld GPS locations within each bin (relative to total locations) and availability equaled the proportion of area within each bin (relative to total area). Selection ratios also determined the subsequent break points for final resource layer classes.

To develop the initial resource map and to classify habitat for HexSim we classified the RSF scores into three categories based on habitat selection where 1 = habitat selected less than available (low quality habitat); 2 = selection approximately equal to availability (moderate quality habitat); and 3 = habitat selection greater than available (high quality habitat). We removed non-habitat types of ice, rock, and water bodies larger than $10km^2$. This initial resource map functioned as our post-fire scenario. We also mapped RSF values with the pre-fire data layers to create the "pre-fire" scenario resource map.

<u>Data Layers</u>

Occupancy, reproduction and habitat selection have been documented during several studies that occurred during the 1980-2012 time period in the Okanogan LMZ (Brittell et al. 1989, Koehler 1990, McKelvey et al. 2000, von Keinast 2003, Maletzke 2004, Koehler et al. 2008, Vanbianchi 2015). These studies and work in other ecosystems (Squires et al. 2010, Squires et al. 2013) provided a group of variables we used in our suite of models to describe habitat. Our final set of variables included those that provided a direct measurement (i.e. canopy cover) as well as those that could be considered as an index or surrogate (i.e. greenness and solar radiation). Our static terrain variables included slope, elevation, aspect, surface ruggedness, topographic wetness index and solar radiation derived with a Digital Elevation Model (smoothed to remove banding. See Copeland et al. 2007) in ARCGIS. We linearized aspect (McKelvey et al. 2000) to provide values that ranged from 0 on the coldest, wettest slopes (due northeast) to 180 on the warmest, driest slopes (due southwest).

We also considered dynamic variables that could potentially capture changes in habitat over time, such as increases due to succession, or decreases due to disturbances such as wildfire, insects and disease or harvest. Our dynamic variables included greenness, vegetative cover type (forest structure type) and canopy cover. Greenness is an index of leafy green productivity calculated with a tasseled cap transformation (Baig et al. 2014). We derived greenness from Landsat 8 imagery during the summer of 2000 and 2013. These two time periods provided the most recent comparable imagery of good quality for the Okanogan and Kettle LMZs that coincided with vegetative data for the post-fire time period as well as a comparable pre-fire snapshot. Vegetative classification was based on GNN data from 2000 and 2012 (Ohmann et al. 2011). We reclassified the original GNN forest type into four categories: mesic-forest (i.e. Engelmann spruce, lodgepole, ABLA dominated), dry forest (i.e. PSME & PIPO dominated), Other forest and Non-forest (i.e. agricultural lands, remnant forest with <10% canopy, grasslands, wet and mesic shrublands and shrub-steppe) (Table 1). Canopy cover data was obtained from the GNN dataset. We included quadratic forms for canopy cover and elevation in some models. For the sake of simplicity the resource maps developed for the post-fire analysis are referred to as “2013 post-fire”.

Table 1. Variables used in resource selection function development.

Category	Variable	Units
Vegetation	Canopy Cover	continuous
	Dry Forest	categorical
	Mesic Forest	categorical
	Other forest	categorical
	Non-forest	categorical
Ecological	Greenness	continuous
	Solar radiation	kj/m2
	Elevation	meters
	Slope	degrees
	Aspect	continuous
	Surface Roughness	ratio

Wildfire and other changes to habitat

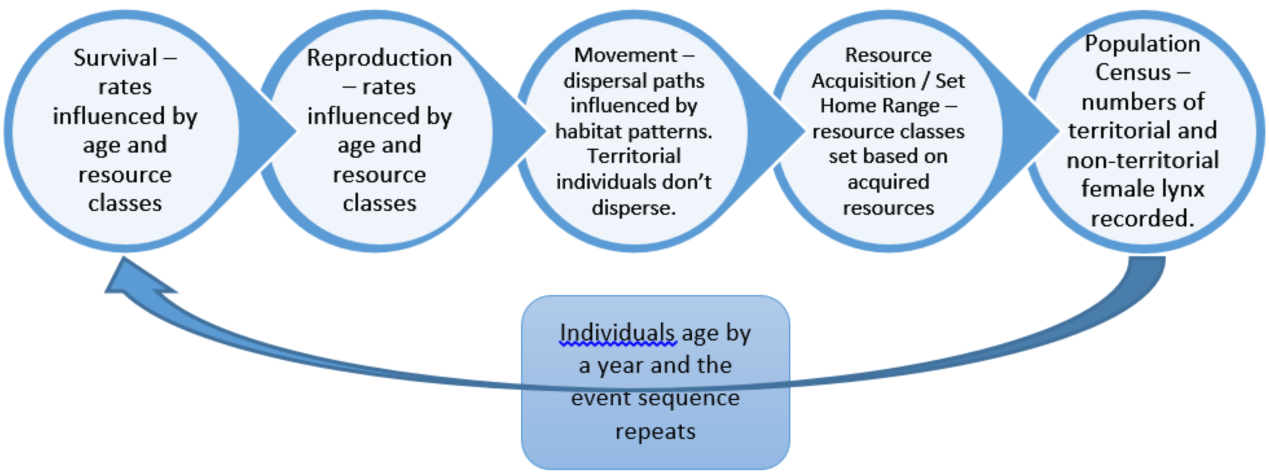
By using Landsat and GNN data from 2000 as compared to 2013 we hoped to capture changes in vegetation due to fires over a 13 year period. This would capture effects from approximately 2000 km^2 of wildfire on the OLMZ. Most of the wildfire activity on the OLMZ after 2013 occurred outside of lynx habitat and burn intensity data was unavailable at the time of this assessment so was not included here (Fig. 5).

In contrast, substantial fire activity within lynx habitat on the Kettle LMZ occurred in 2015. As such we adjusted the 2013 resource layer for the Kettle to account for those changes (see below under Kettle LMZ Resource Layer development). Wildfire impacted approximately 360 km^2 on the Kettle LMZ from 2000 through 2015. We attempted to use the best available data consistently across the LMZs to describe the current habitat condition but did not want to disregard the significant recent fire activity on the KLMZ.

Carrying Capacity Model – HexSim Input

HexSim is an individual-based population modeling framework that represents population function based on a series of annual life history events. The Canada lynx model incorporated survival, reproduction, movement, resource acquisition, home range establishment and a population census, all of which are influenced by habitat conditions. We used a female-only, single-sex model structure because: 1) lynx are polygynous, 2) reproductive output is limited by the number of females of reproductive age, 3) female survival influences population trend more than male survival (Aubry et al. 2000, Anderson and Lovallo 2003) and 4) to reduce the complexity of the model. Model parameters were based on local empirical information, estimates from the literature or professional opinion depending on availability of information.

Figure 3. HexSim flowchart – HexSim is an individual-based population modeling framework that represents population function based on a series of annual life history events. Events in the lynx model included: 1) Survival, 2) Reproduction, 3) Movement, 4) Resource Acquisition / Home Range Establishment, and 5) Population Census. The process repeats as individuals age by a year.



Habitat Resources

HexSim uses a hexagonal grid to represent habitat conditions that influence individual movement, survival, and reproduction. The Okanogan and Kettle landscapes were represented as a grid of 16.2 ha (500m diameter) hexagons. We chose this hexagon size because it captured relatively fine-scale landscape patterns that we expect would influence lynx habitat selection without becoming computationally limiting. Each hexagon was assigned a resource score based on underlying habitat values. We calculated a focal sum of Habitat Classes 1 (poor quality) through 3 (high quality) at a 250m radius across the study area. We attributed hexagons with the focal sum value at the center of the hexagon. Simulated individuals were assigned to a resource quality class based on the total resource scores of all hexagons within their home ranges (see Resource Acquisition / Home Range section below).

Survival

Survival rates of females were incorporated into the model relative to age class and resource quality. Modeled individuals were assigned to four age classes: kitten (<1 year), yearling (age 1 year), sub-adult (age 2 years) and adult (age >2 years). Survival values for each age class were estimated based on data available from other lynx populations. Although there were extensive data available in the literature relative to survival estimates for the four age classes, (kitten, yearling, subadult and adult), no quantifiable information on the relationship between survivorship and habitat quality was available. As such we estimated female survival for kittens, yearlings, subadults, and adults in low, moderate and high quality habitat based on general published values. We determined the values for each life stage in the high habitat quality class as the highest values from our literature review less 5%, in the moderate habitat quality class as the mean value from the literature, and in the low habitat quality class as 25% less than the lowest value in the literature (Table 2). The resource quality class refers to lynx whose home range meets the home range requirements as defined in HexSim. A home range in the high resource quality class had a minimum of 60% of the home range in the high quality category. A home range in the Moderate resource quality class had 40 to 59% of the home range in the high quality category. Home ranges that did not meet the high or moderate classes defaulted to the low resource quality class.

Table 2. Annual female lynx survival values for all combinations of age classes and resource quality classes used in population model. Values were determined for each life stage in the high habitat quality class as the highest value from our literature review less 5%, in the moderate habitat quality class as the mean value from the literature, and in the low habitat quality class as 25% less than the lowest value in the literature.

	Resource Quality Class		
Age Class	Low	Moderate	High
Kitten	0.09	0.45	0.74
Yearlings*	0.39	0.60	0.65
Sub-adult	0.39	0.60	0.65
Adult	0.56	0.85	0.88

*data specific to yearlings was unavailable in the literature so were set equal to sub-adults.

Reproduction

Like many aspects of lynx population dynamics, lynx reproduction is closely tied to hare populations and will fluctuate according to hare density (Aubry et al. 2000). Lynx have a moderate reproductive rate, resulting primarily from the early age of first reproduction (as early as one year old), a litter size that generally ranges from 1-4 kittens and a short interval between litters (at most annually, but interval may increase dependent on prey densities) (Brittell et al. 1989, Koehler 1990, Brainerd 1985, Squires 2016). Fecundity in lynx is defined as the average number of young per adult female per year. Fecundity values were estimated based on data available from other lynx populations. In our model only yearling, subadult, and adult females with home ranges that met the moderate or high habitat quality class as defined in HexSim were allowed to reproduce. Similar to the survival estimates, we determined fecundity rates in the high habitat quality class as the highest value from our literature review less 5%, in the moderate habitat quality class as the mean value from the literature, and zero in the low habitat quality class (Table 3). The age of first reproduction was set at one year.

Table 3. Annual female lynx fecundity values for all combinations of age classes and resource quality classes used in population model. Values were determined for each life stage in the high habitat quality class as the highest value from our literature review less 5%, in the moderate habitat quality class as the mean value from the literature, and in the low habitat quality class as 25% less than the lowest value in the literature.

	Resource Quality Class		
Age Class	Low	Moderate	High
Kitten	0	0	0
Yearling*	0	0.15	0.29
Sub-adult	0	0.15	0.29
Adult	0	0.83	1.20

*data specific to yearlings was unavailable in the literature so were set equal to sub-adults.

Movement

Movement parameters for dispersing individuals were based on information from other lynx populations and data from the OLMZ. Published information on female lynx dispersal is limited in southern boreal forests (Aubry et al. 2000) and available information in other ecosystems suggests a wide range of possibilities (Poole 1997, Mowat et al. 2000). Although information has been recorded on long-distance movements, female lynx may not disperse long distances, and may establish home ranges that are near or overlap their natal home range (Aubry et al. 2000, Mowat et al. 2000). We calculated mean home range diameters for female lynx in the OLMZ of approximately 13km. As such we set the dispersal value as 11km to allow lynx to disperse but still allow for overlap. Only individuals that failed to acquire adequate resources to establish a home range dispersed. Generally we assumed that lynx were dispersal habitat generalists and were not strongly influenced by habitat suitability in their dispersal movements. Marcot et al. (2015) found that HexSim population estimates had relatively low sensitivity to dispersal movement parameters compared to other model parameters they investigated.

Resource Acquisition and Home Range

Home Range

To determine the home range sizes for HexSim scenarios we calculated 95% minimum convex polygon home ranges (Calenge 2006) for female lynx in the OLMZ and also used values from lynx work completed earlier in the analysis area (Koehler 1990). As such the home-range sizes used in the carrying capacity models were 39km^2 (Koehler 1990), 55km^2 (mid-range value) and 72km^2 (the mean OLMZ female home range estimate). In our model, individual lynx were classified as group members (female lynx with established home ranges), or floaters (dispersing female lynx without home ranges).

Territoriality

Although lynx may have home ranges that overlap, the degree of overlap, or territoriality, often depends on the sex of the individuals. Related females and opposite sex tend to be more tolerant of overlap (Poole 1995, Mowat et al. 2000). We incorporated territoriality by requiring lynx to defend a proportion of their home range, thus preventing other lynx from using those resources. Quantitative data on territoriality is limited so we analyzed the spatial and temporal overlap of female lynx in the OLMZ with a straightforward method. We estimated a 60% fixed kernel core home range and then examined the degree of overlap. We found female lynx (n=2) that exhibited spatial and temporal overlap had 79 – 87% overlap of the core home range. We also examined model sensitivity to territoriality values and found population size increased to an optimal value when territoriality was equal to 30%. As territoriality increased the population size and variability decreased. For our scenarios we set territoriality at 30%, recognizing that this would optimize population densities and values will vary depending on actual defended territory.

<u>Carrying Capacity Model –Scenarios</u>

Because data on lynx demographics and habitat use can vary considerably, we created several different model scenarios to examine carrying capacity of the Okanogan and Kettle LMZs and the influence of disturbance. We developed multiple scenarios to assure key model variables were included and to address the uncertainty associated with modeling a potential population. A complete description of all model input is provided in Appendix S1.

Our preliminary analysis resulted in a suite of three different model scenarios that we believed were most plausible and likely bound the actual carrying capacity of the OLMZ (Table 4). Each model was run for a total of 175 years, including a 75 year "burn-in" period followed by a 100 year simulation period. Models were initiated with 1000 individuals randomly placed across the landscape. The "burn-in" period allowed populations to approach equilibrium in the landscape and develop a representative distribution of age classes prior to the simulation period (Singleton 2013). We ran the three scenarios on the 2013 post-fire resource map and on the 2000 pre-fire resource map to examine effects of habitat changes on population outcomes. However, it should be noted that the two different time steps are represented by snapshots of habitat quality at defined intervals. The model outputs are best interpreted as indices of habitat carrying capacity under landscape conditions at two specific times, given model uncertainty and assumptions.

Table 4. Description of model scenarios developed to estimate carrying capacity for lynx in the OLMZ. The number in the Scenario name refers to the home range size used in the model. All models used the same initial resource layer as indicated by pre-fire or post-fire.

Scenario	**Description**
39_pre-fire	39 km^2 home range size. Resource layer to describe pre-fire habitat conditions in 2000.
39_post-fire	39 km^2 home range size. Resource layer to describe post-fire habitat conditions in 2013.
55_pre-fire	55 km^2 home range size. Resource layer to describe pre-fire habitat conditions in 2000.
55_post-fire	55 km^2 home range size. Resource layer to describe post-fire habitat conditions in 2013.
72_pre-fire	72 km^2 home range size. Resource layer to describe pre-fire habitat conditions in 2000.
72_post-fire	72 km^2 home range size. Resource layer to describe post-fire habitat conditions in 2013.

We ran 25 population simulation replicates per scenario. Preliminary analysis indicated that 25 replicates were adequate to capture the variability in annual population size and distribution estimates produced by repeated simulations. We used simulation-duration mean number of individuals to represent the carrying capacity metric. We summarized patterns of spatial distribution of the modeled populations across the LMZ by calculating the annual mean number of female lynx with home ranges by LAU. All model output compilation, statistical analysis and mapping were conducted using R software (version 3.2.2, R Development Core Team, Vienna, Austria) and ArcGIS (version 10.4, ESRI, Inc.).

To calibrate our model results we compared our population outcomes with previously calculated density estimates for the OLMZ and other similar ecosystems. We calculated a population size for each LMZ where: population size = density estimate from literature (#lynx /100km^2) * LAU area (100km^2). Although these other ecosystems may not be at carrying capacity, a comparison of density estimates provided a plausibility test of model outcomes.

Resource Layer and Carrying Capacity Model – Kettle LMZ

Because site specific information on lynx in the Kettle LMZ is unavailable, we applied the Okanogan LMZ model to the Kettle LMZ landscape. We developed the resource layer using the same spatial data sources, specific to the Kettle region. To account for the 2015 fire activity and to provide a more accurate representation of the current situation, we adjusted the initial RSF output with recent fire activity data. We overlayed Rapid Assessment of Vegetation Condition after Wildfire (RAVG) data from the US Forest Service to discount RSF values within fire boundaries in 2015 (http://www.fs.fed.us/postfirevegcondition/whatis.shtml).

RAVG provided a seven-class basal area loss layer (Table 5) that was used to adjust the Kettle 2015 Resource Map. For the purposes of this exercise, areas within RAVG Classes 1 and 2 did not change the resource map habitat class. Areas within RAVG Class 3 decreased the resource map habitat class by 1 (from high quality to moderate quality habitat or from moderate quality habitat to low quality habitat). Areas within RAVG Classes 4-7 decreased the resource map habitat class to Class 1-low quality habitat.

Table 5. Rapid Assessment of Vegetation Condition after Wildfire (RAVG) classes and associated loss of basal area vegetation resulting from wildfire.

RAVG Class	% basal area loss
1	0
2	0 - < 10
3	10 - < 25
4	50 - < 75
5	25 - < 50
6	75 - < 90
7	90 or greater

RESULTS and DISCUSSION

Lynx Habitat Modeling – Okanogan and Kettle LMZs

The most parsimonious RSF habitat model contained greenness, mesic forest, non-forest, surface ruggedness, aspect, elevation and canopy cover and the quadratics for elevation and canopy cover (Table 6.). This RSF model had considerably greater empirical support as compared to the remaining models (second "best" model ΔAICc =30). Habitat selection results indicated a positive relationship with greenness, mesic forest, non-forest, elevation and canopy cover, a negative relationship with aspect, surface ruggedness and a quadratic effect for elevation and canopy cover. Correlations between surface ruggedness and slope and between aspect and solar radiation eliminated pairing of these variables in subsequent models.

Table 6. Parameters and associated coefficients in the Okanogan LMZ habitat model.

Fixed Effects			95% Confidence Interval	
	Estimate	Standard Error	Lower	Upper
greenness	0.39	0.01	0.29	0.47
mesic forest	0.44	0.03	0.29	0.59
non-forest	2.18	0.08	1.58	2.79
surface ruggedness	-0.6	0.02	-1.04	-0.17
aspect	-0.18	0.01	-0.26	-0.1
elevation	15.54	0.28	11.83	20.26
elevation^2	-13.29	0.24	-17.57	-10.08
canopy cover	3.06	0.10	1.96	4.19
canopy cover^2	-2.18	0.08	-3.08	-1.15
Intercept	-4.3	0.13	-5.14	-3.36

Selection ratios from model development and evaluation datasets indicated that the threshold for habitat selection occurred when transformed RSF scores were ≥0.4. We looked at selection of individual lynx to determine classification and categorized the resource layer map as follows:

- Class 1 = RSF score <0.4. Selection less than available (poor quality lynx habitat)
- Class 2 = RSF score ~0.4-0.5. Selection equal to or slightly greater than available (moderate quality lynx habitat).
- Class 3 = RSF score >0.5. Selection greater than available (high quality lynx habitat).

Eighty-seven percent of withheld lynx locations had RSF values ≥0.4 (moderate to high quality habitat), whereas only 36% of the model development area had values ≥0.4. The resulting resource maps depict relative quality of habitat across the LMZ in the pre-fire (Fig 4a) and post-fire (Fig. 4b) time periods. Approximately 260 km^2 (3%) of lynx habitat in the OLMZ decreased from high quality habitat (Class 3) to low quality habitat (Class 1), primarily as a result of wildfire.

Our resource maps provided a reasonable and consistent general description of lynx habitat selection in the Okanogan analysis area. Previous studies in the Okanogan area found lynx select for Engelmann spruce and subalpine fir forest, moderate canopy cover, flat to moderate slopes, and relatively high elevations; and select against Douglas-fir and ponderosa pine forests, forest openings, recent burns, sparse canopy and understory, and relatively steep slopes (Koehler et al. 2008, Maletzke et al. 2008).

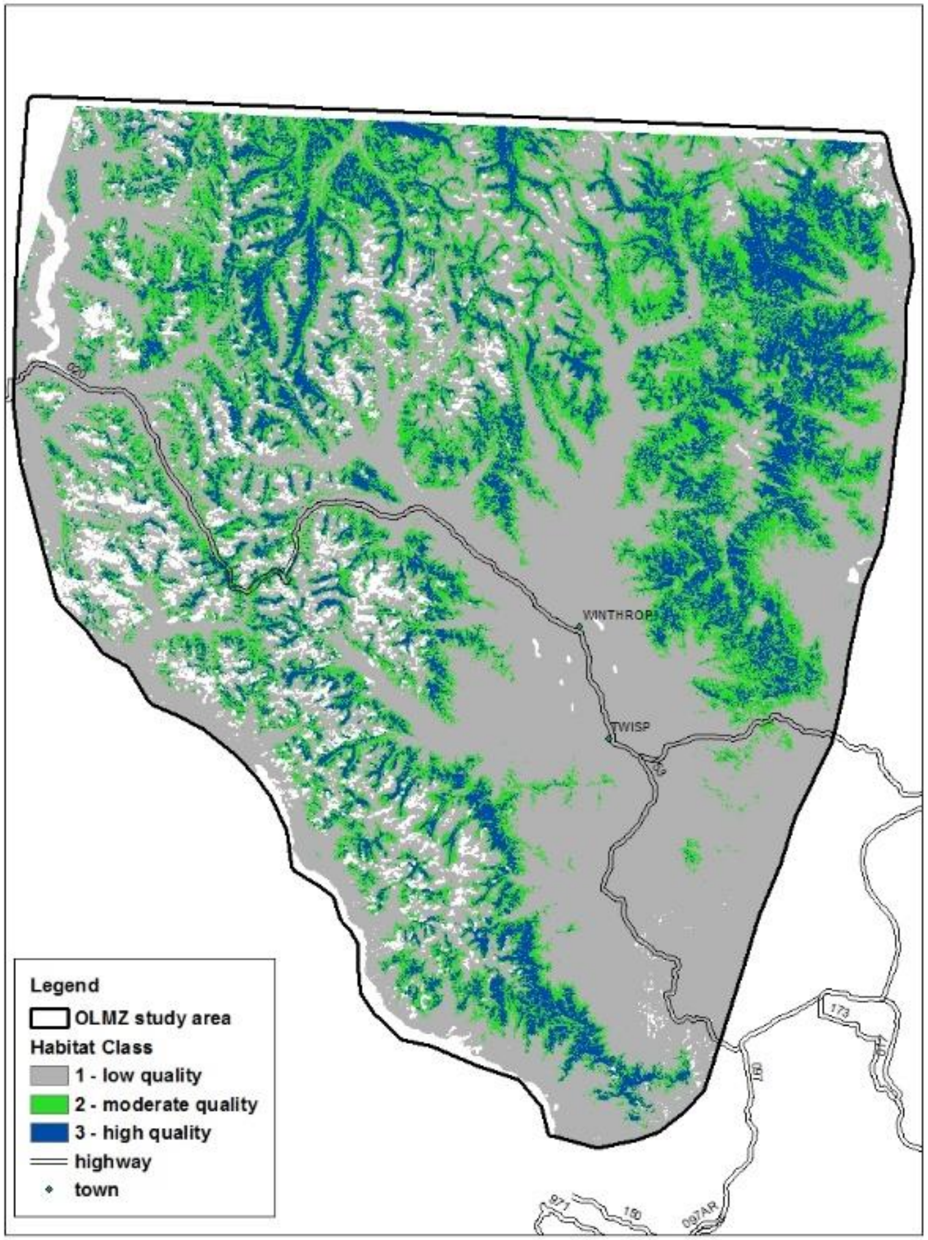
Other studies have shown quality foraging habitat for lynx occurs where forest structure provides habitat for snowshoe hares (Koehler 1990, Agee 2000, Hodges 2000) in the form of dense, multi-layered understory (Hodges 2000, Lewis et al. 2011) that maximizes cover and browse at varying snow depths throughout the winter. Such habitat structure is common in early-seral stages but may also occur in coniferous forests with mature but relatively open overstories (Hodges 2000, Lewis et al. 2011). Another important component of lynx habitat is areas that are used for denning (Koehler 1990, Moen et al. 2008, Squires et al. 2008) which generally consists of large woody debris, in the form of either down logs or root wads (Koehler 1990, Mowat et al. 2000, Slough 1999, Squires et al. 2008). These structures are often associated with late-successional forests and may be located within older regenerating stands (>20 years since disturbance) or in mature conifer or mixed conifer-deciduous (typically spruce/fir or spruce/birch) forests (Koehler 1990, Slough 1999, Squires et al. 2008). Lynx habitat selection was strongly associated with elevation as lynx are highly adapted to environments that receive considerable winter snowpack (Koehler and Aubry 1994, Aubry et al. 2000, von Keinast 2003, Maletzke 2004). Recent research in the Okanogan area indicated that lynx avoid recently burned areas, particularly areas that burned with higher intensity, but may use unburned stands within fire boundaries (Vanbianchi 2015). These "skips" may provide connectivity across large burned areas. It should be noted that lynx survivorship, productivity and population dynamics are closely related to snowshoe hare density, although potentially to a lesser degree in the southern boreal forests (Aubry et al. 2000, Mowat et al. 2000), but subsequent model complexity and a lack of data prohibited including prey density in our model.

Kettle LMZ Resource Layers

Application of the RSF model to the Kettle LMZ suggested lynx habitat is primarily located along the center of the LMZ where elevations and habitat types fall into those preferred by lynx. (Fig. 6a and 6b). Approximately 95 km^2 (3%) of lynx habitat in the KLMZ decreased from high and moderate quality habitat (Class 3 and 2) to low quality habitat (Class 1), primarily as a result of wildfire.

Figure 4. Annual mixed effect resource selection function reclassified to relative habitat quality classes mapped within the Okanogan Lynx Management Zone. 4a) depicts the 2000 pre-fire condition, prior to substantial wildfire activity from 2000-2013, while 4b) depicts the 2013 post-fire condition.

4a) 2000 pre-fire



4b) 2013 post-fire

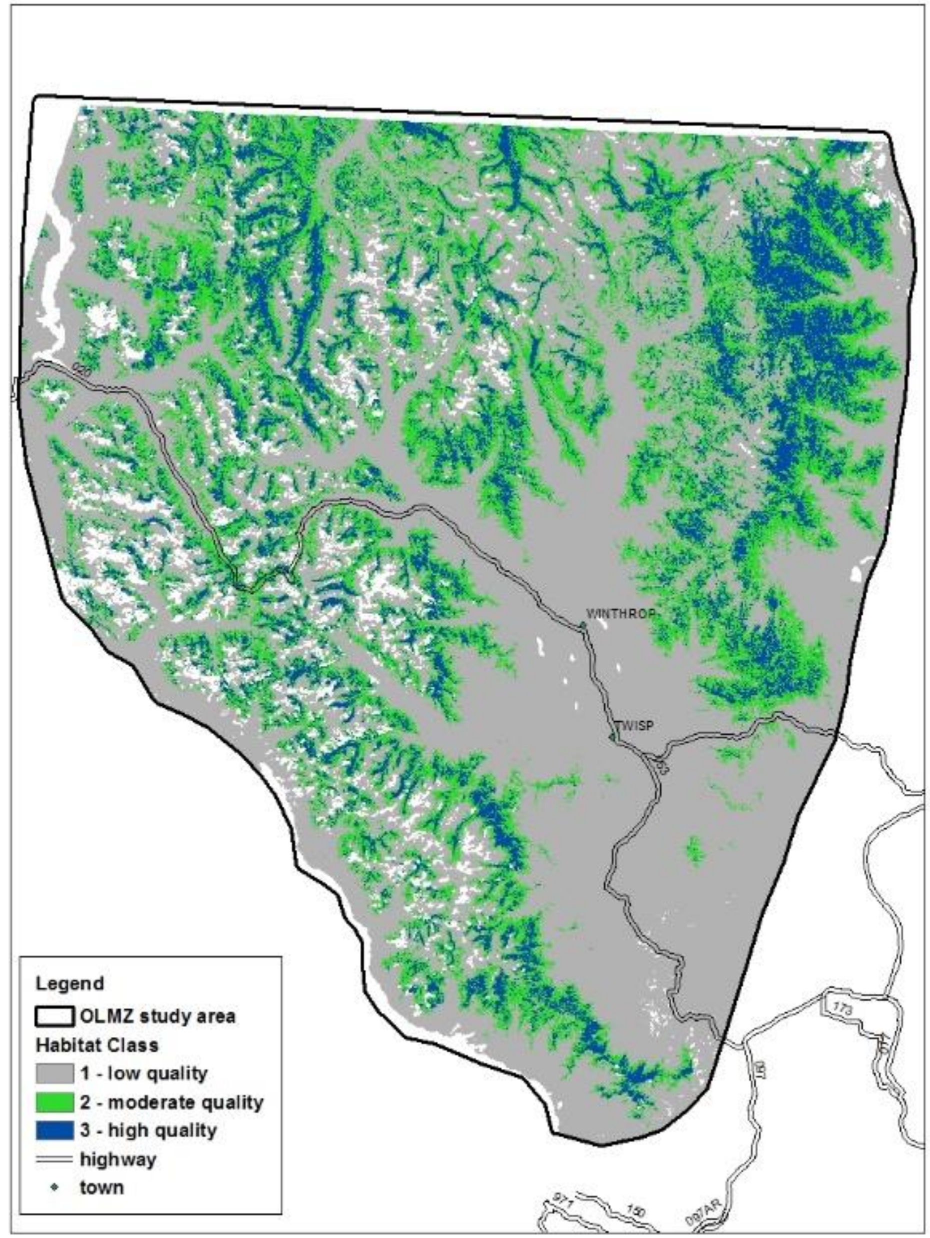


Figure 5. Okanogan Lynx Management Zone post-fire resource map with fire activity polygons from 2000-2015. The majority of fire activity after 2013 occurred outside of lynx habitat and burn intensity data was unavailable at the time of this assessment so was not included here.

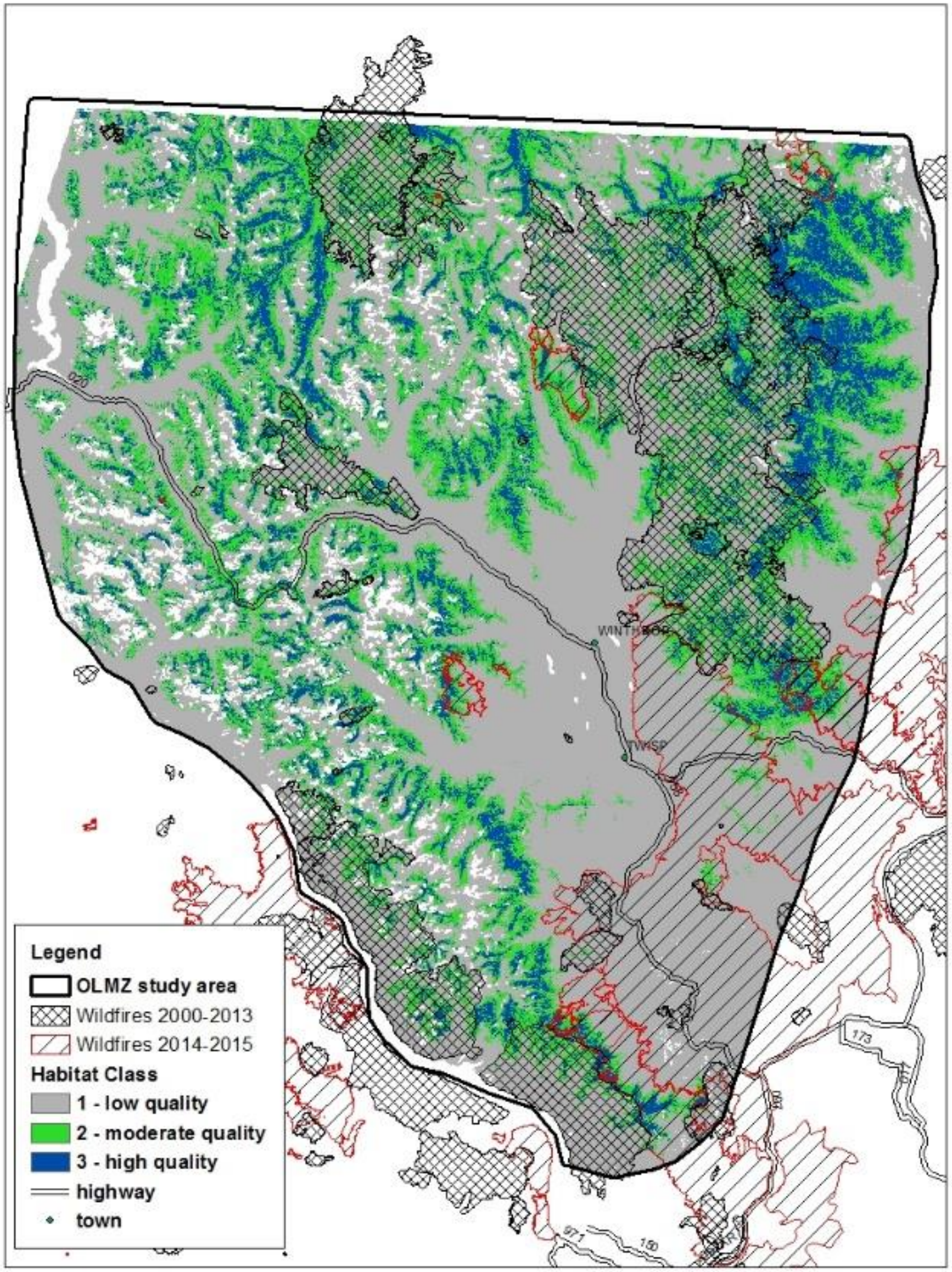
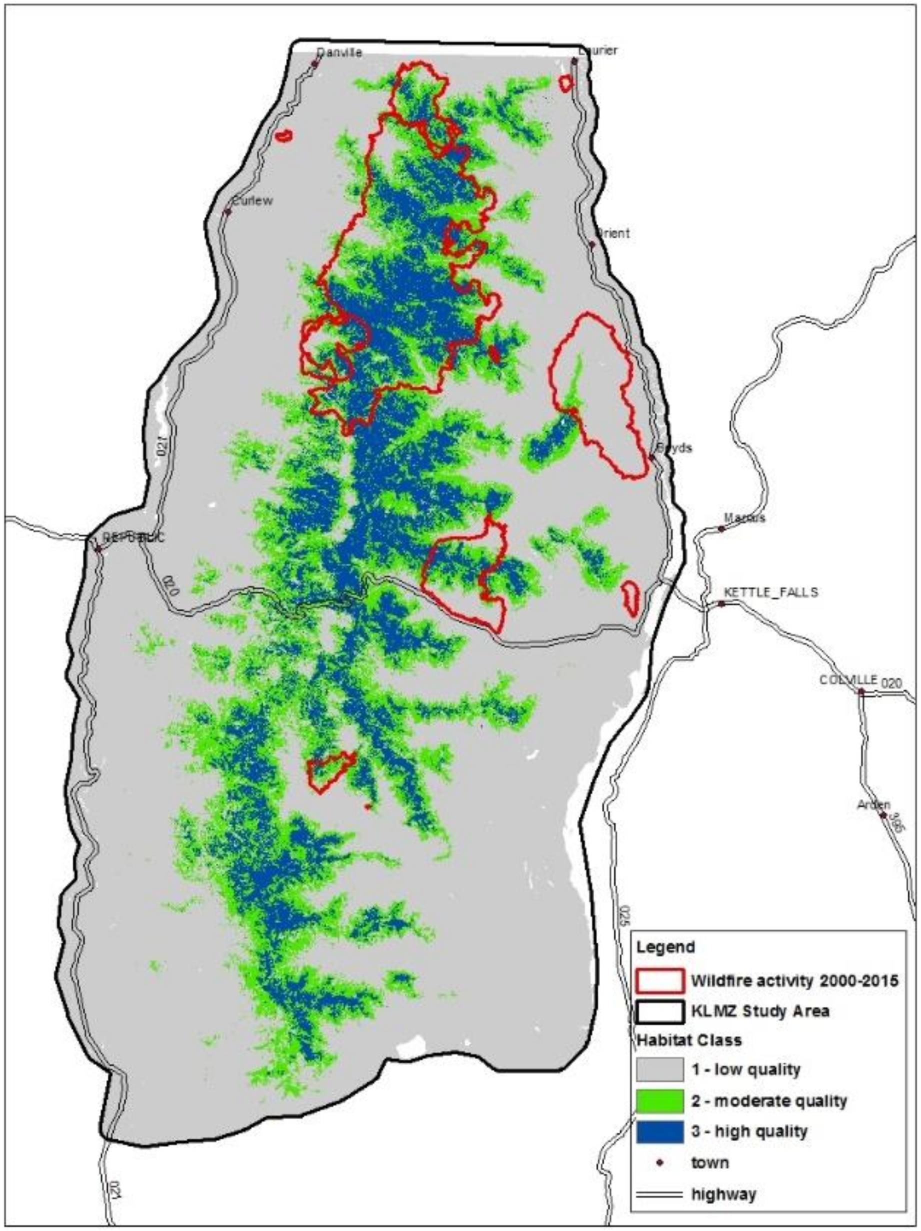
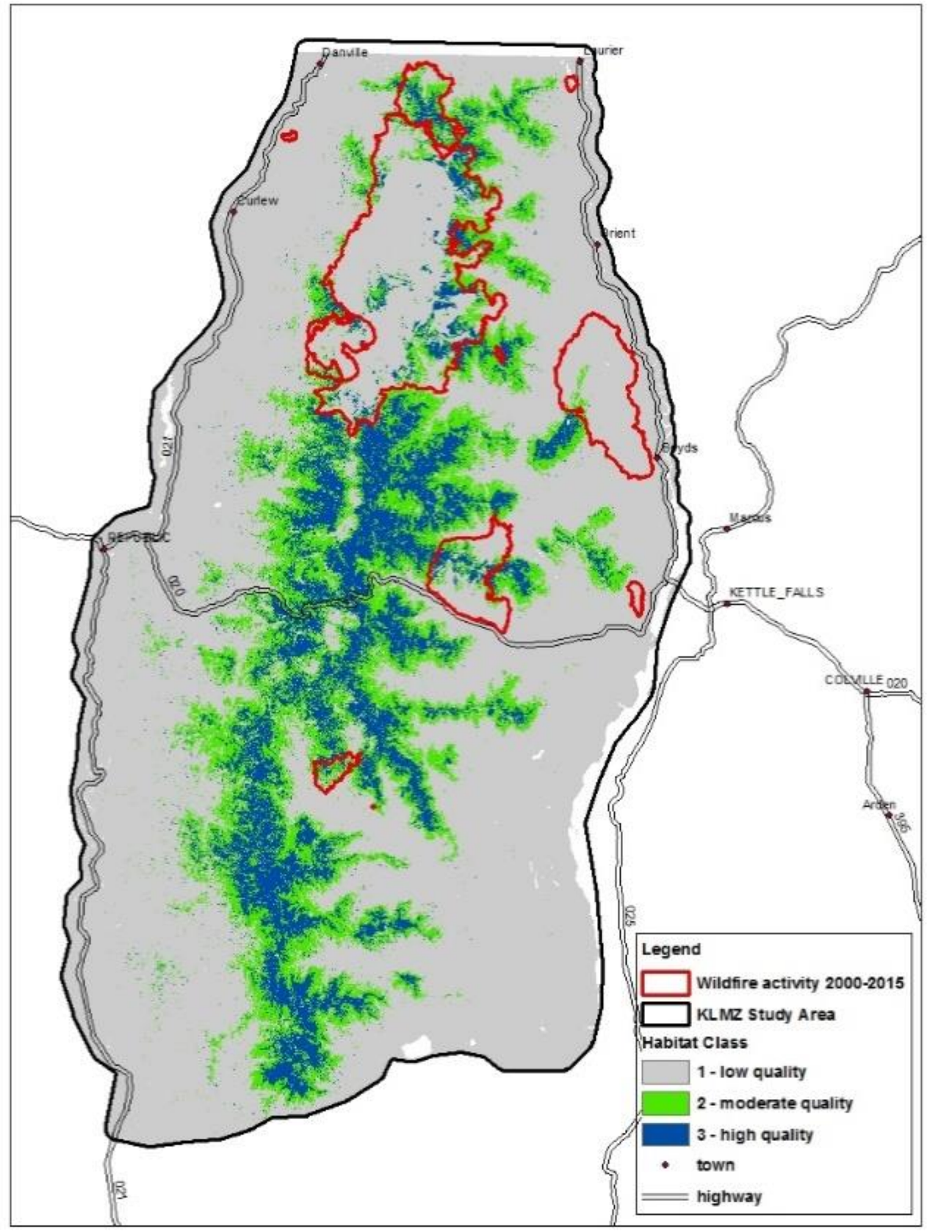


Figure 6. Annual mixed effect resource selection function reclassified to relative habitat quality classes mapped within the Kettle Lynx Management Zone. 6a) depicts the 2000 pre-fire condition prior to substantial wildfire activity from 2000-2015, while 6b) depicts the 2015 post-fire condition. Red polygons depict fire boundaries for wildfire activity from 2000 through 2015.

6a) 2000 pre-fire



6b) 2015 post-fire



Carrying Capacity Estimates – Okanogan and Kettle LMZs

The range of model outcomes for the pre-fire time period indicated the OLMZ was capable of supporting a lynx population that ranged from a low of four females to a high of 70 females (Table 7). Results varied greatly depending on the home range size and, as expected, larger home ranges resulted in smaller carrying capacity estimates. The HexSim modeling framework also demonstrated the negative impact that wildfire has on carrying capacity for lynx. Habitat changes due to wildfire resulted in a reduction in total female population estimates ranging from 36-68% (Table 7) as compared to the pre-fire scenarios. Several simulations reached a population size of zero before the completion of the run. This suggests that the LMZ may not be capable of sustaining a lynx population in isolation and may be dependent on immigration, particularly given larger home range size assumptions.

The Kettle LMZ displayed similar results. The range of model outcomes for the pre-fire time period indicated the KLMZ was capable of supporting a lynx population that ranged from a low of three females to a high of 24 females (Table 7). Results varied greatly depending on the home range size and, as expected, larger home ranges resulted in smaller carrying capacity estimates. Habitat changes due to wildfire resulted in a reduction in total female population estimates ranging from 30-52% (Table 7) as compared to the pre-fire scenarios. Only the 39_prefire scenario replicates reached simulation completion each time, suggesting the KLMZ may be even more limited than the OLMZ with regard to sustaining a lynx population in isolation.

Model Calibration: Are these estimates plausible?

Our simulation results provided a range of potential lynx carrying capacity values for the Okanogan and Kettle LMZs. To examine if these estimates were plausible we compared our results to density estimates from a variety of other ecosystems. Density estimates ranged considerably depending on the ecosystem (i.e. northern boreal vs. southern boreal) and snowshoe hare density. As such our population estimate comparisons may be conservative. For this exercise we compared our estimates to those of southern boreal forests such as the Okanogan (Brittell et al. 1989, Koehler 1990), or more northerly ecosystems during low hare density years such as the Yukon (Slough and Mowat 1996) and the NW Territories (Poole 1994), which provided a range of densities from 2 – 3 lynx /100km^2.

Based on those densities reflected in the literature we estimated approximately 60-91 females within the Okanogan LMZ. Our post-fire simulations resulted in population estimates that ranged from 1-45 females in the OLMZ, which was slightly lower than the range estimated from other Washington studies or ecosystems. Based on those densities reflected in the literature we estimated approximately 10-15 females within the Kettle LMZ. Our post-fire simulations resulted in population estimates that ranged from 1-16 females in the KLMZ, which was similar to the range estimated from other Washington studies or ecosystems.

Spatial patterns of lynx occupancy within both LMZs were generally consistent across the model variants (Fig. 7 and 8). Lynx were predicted to occur throughout the LAUs within the LMZs in the pre-fire scenarios, while LAUs in the current scenarios occasionally equaled zero. Predicted lynx abundance generally followed the pattern of the resource map with higher densities occurring in areas of contiguous higher quality habitat, and then shifted with the post-fire resource layer and correlated with the location of large wildfires that occurred from 2000-2015.

Okanogan LMZ

LAUs on the east side of the ecosystem (Loomis Central/North/South) and in the Pasayten Wilderness generally had the highest density of territorial females across pre-fire scenarios (Fig. 7). Including the influence of habitat changes decreased overall densities throughout the LMZ. Some LAUs with substantial fire activity reached densities of zero. These patterns were relatively consistent across scenarios.

Kettle LMZ

Lambert, Indian and U.S. LAUs generally had the highest density of territorial females across pre-fire scenarios (Fig. 8). This seemed reasonable given the high quality habitat mapped by the RSF model along the central portion of the LMZ. However, including the influence of habitat changes decreased overall densities throughout the LMZ. Lambert and North Sherman LAUs, centrally located in the LMZ, had the highest post-fire densities. The lowest density LAUs were on the north end of the LMZ where the majority of the wildfire impacts occurred. These patterns were relatively consistent across scenarios.

The spatial distribution estimates along the international border may be somewhat inaccurate because our analysis area created a false barrier along the northern edge where hypothetical lynx could not disperse and habitat values diminished. This was an artifact of our model framework that could be addressed by expanding the spatial extent of the model into Canada. This approach should be considered as our simulations indicated these populations are likely dependent on immigration from BC for persistence. Because habitat is limited, lynx populations in the US are small relative to the larger populations in Canada. As such US lynx populations may depend on immigration from populations in Canada to ensure genetic diversity and population persistence (Ruggiero et al. 2000). Koehler et al. (2008) discussed how trapping, wildfire and timber harvest contributed to decreased lynx populations in the Okanogan and Kettle regions over 10 years ago. The challenges associated with these LMZs, such as isolated habitat, increased wildfire, and potential dispersal obstacles (fencing, major roadways), are still significant conservation challenges.

Conclusion

Through modeled simulations we have estimated the carrying capacity of lynx in the Okanogan and Kettle Lynx Management Zones, which can inform efforts to manage lynx in these ecosystems. Lynx populations in Washington have experienced a decline over the past 20 years that can be partially attributed to the loss of quality habitat to wildfire. Our modeling approach involved estimating carrying capacities for two landscapes that received no immigration from outside population sources. Using this approach, the small carrying capacities we estimated may correspond to low probabilities of persistence until habitat conditions in these LMZs could support larger populations. However, the lynx population in Washington is not isolated and because it is on the margin of their range, the connection with the larger population to the north in Canada is likely sustaining the Washington population. On-going habitat loss and fragmentation warrants further consideration relative to population persistence. We explored carrying capacity with a single sex model, acknowledging these models have limitations for representing small population processes (including Allee effects and demographic stochasticity) that can contribute to small population extinction and meta-population instability. Additionally, the population we modeled is based on demographic characteristics from resident populations, however the characteristics of the lynx population currently residing in the Okanogan LMZ may differ substantially from a typical resident population. The population's relatively small size, its position at the margin of the range, the possible limitations of demographic support (i.e. immigration) from BC, and the fragmented configuration of habitat within the LMZ, may significantly influence the sex ratio, age structure and reproductive potential of this population, and ultimately, its probability of persistence. As such, creating a two-sex model to simulate population viability would be a logical next step to further assess the stability, viability and probability of persistence of the Washington population to inform recovery objectives and strategies.

Table 7. Simulation-duration annual mean number of female individuals for the total, group and floater populations in the Okanogan and Kettle LMZs for six scenarios. The change in population carrying capacity as a result of changes in habitat due to wildfire and other disturbances, as well as succession, was calculated as the percent change in total population size between scenarios (Post-Fire – Pre-Fire). Group members were female lynx in the total population with established home ranges and floaters were dispersing female lynx in the total population without home ranges.

LMZ	Scenario	Total Population (#)	90% quantile range	SE	Group Members (#)	90% quantile range	SE	Floaters (#)	90% quantile range	SE	Decrease in Population Size (%)	Number of simulations that reached 100 years (out of 25 simulations)	Mean persistence (years)
OKANOGAN	39_pre-fire	70	49-89	0.5	40	29-51	0.3	30	19-40	0.3		25	100
	39_post-fire	45	29-63	0.4	25	16-34	0.2	19	11-29	0.2	36	25	100
	55_pre-fire	39	24-54	0.4	22	14-31	0.2	16	9-24	0.2		25	100
	55_post-fire	21	0-36	0.4	12	0-19	0.2	9	0-17	0.2	46	4	90
	72_pre-fire	4	0-14	0.1	2	0-7	0.1	2	0-7	0.1		3	44
	72_post-fire	1	0-5	0.1	1	0-3	0.03	1	0-2	0.03	68	0	16
KETTLE	39_pre-fire	24	12-35	0.2	14	7-20	0.1	10	4-16	0.1		25	100
	39_post-fire	16	0-28	0.2	9	0-16	0.1	7	0-13	0.1	33	20	87
	55_pre-fire	12	0-22	0.2	7	0-13	0.1	5	0-10	0.1		19	87
	55_post-fire	8	0-19	0.2	5	0-11	0.1	4	0-9	0.1	30	10	72
	72_pre-fire	3	0-9	0.1	1	0-4	0.04	1	0-4	0.04		4	30
	72_post-fire	1	0-5	0.1	1	0-3	0.03	1	0-2	0.04	52	0	4

Figure 7. Spatial distribution of mean annual territorial female lynx density (# per 100km^2) by LAU in the Okanogan LMZ. Differences between scenarios were a result of resource changes due to disturbance, primarily wildfire, with three different home range sizes (39km^2, 55km^2, and 72 km^2). Color scheme and range of values were held constant within each home range to show the influence of disturbance on modeled density outcomes.

Home Range: 39km^2

Scenario: 39_pre-fire

Scenario: 39_post-fire

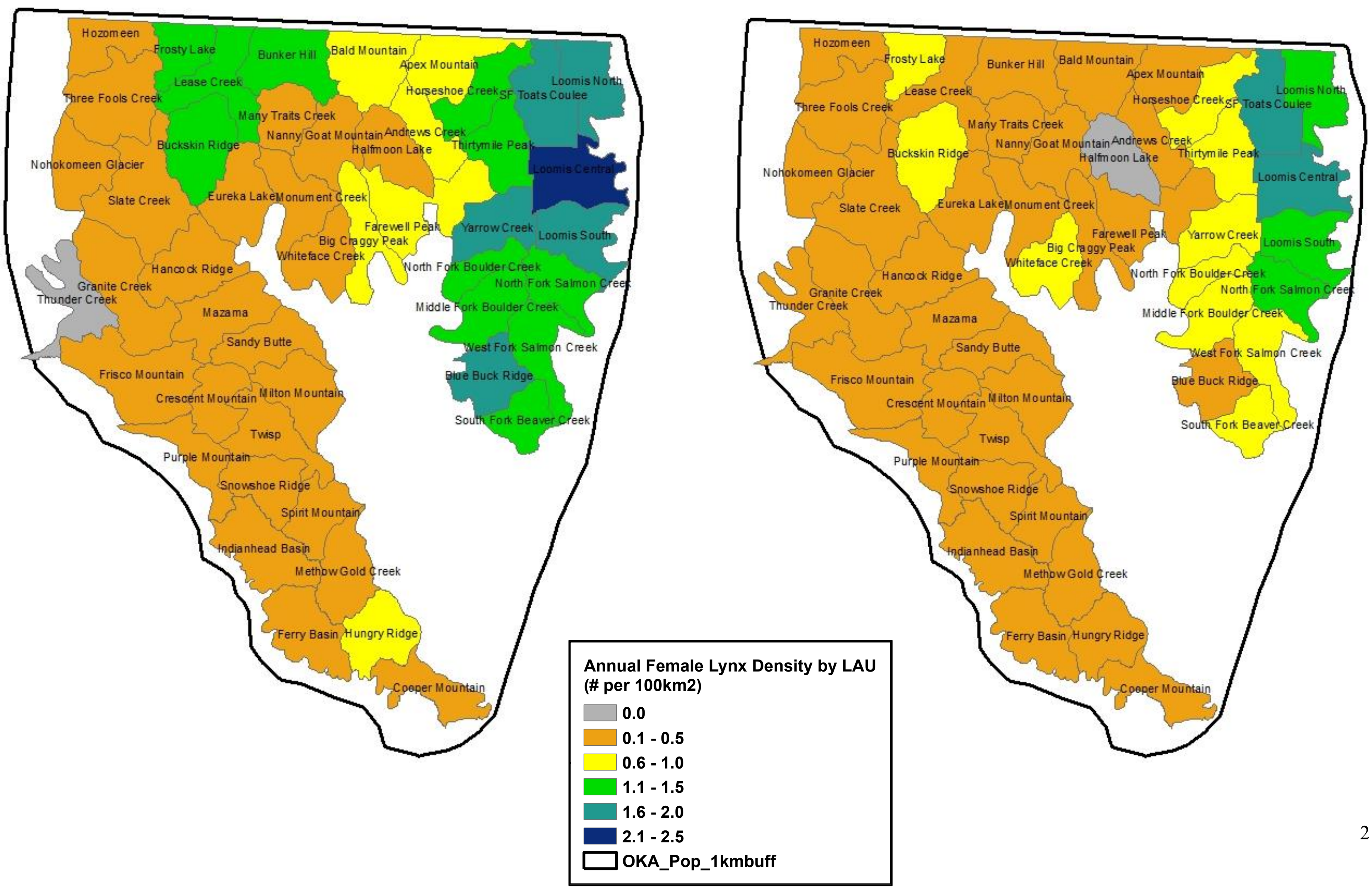


Figure 7. continued

Home Range: 55km^2

Scenario: 55_pre-fire

Scenario: 55_post-fire

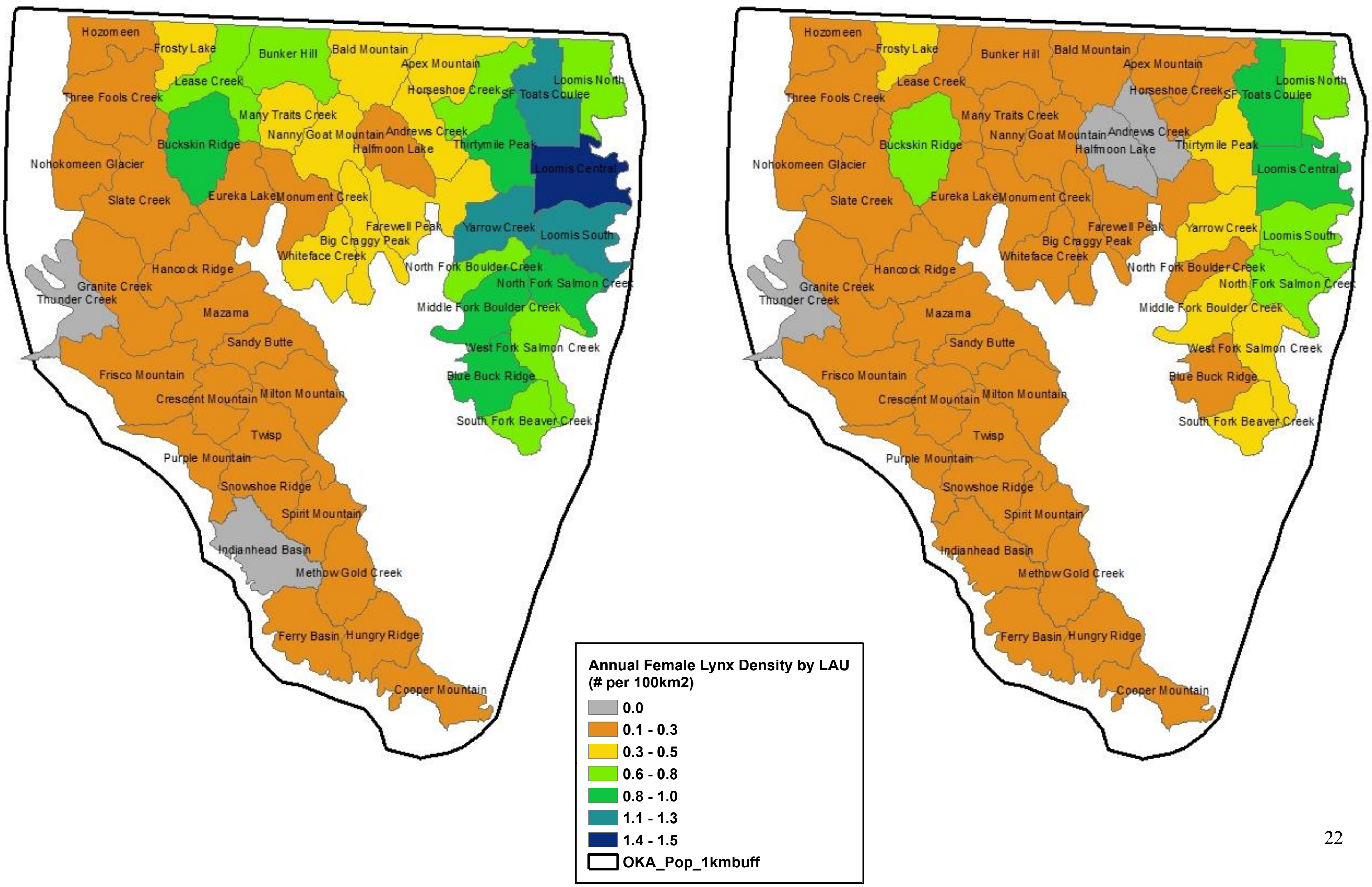


Figure 7. continued

Home Range: 72 km^2

Scenario: 72_pre-fire

Scenario: 72_post-fire

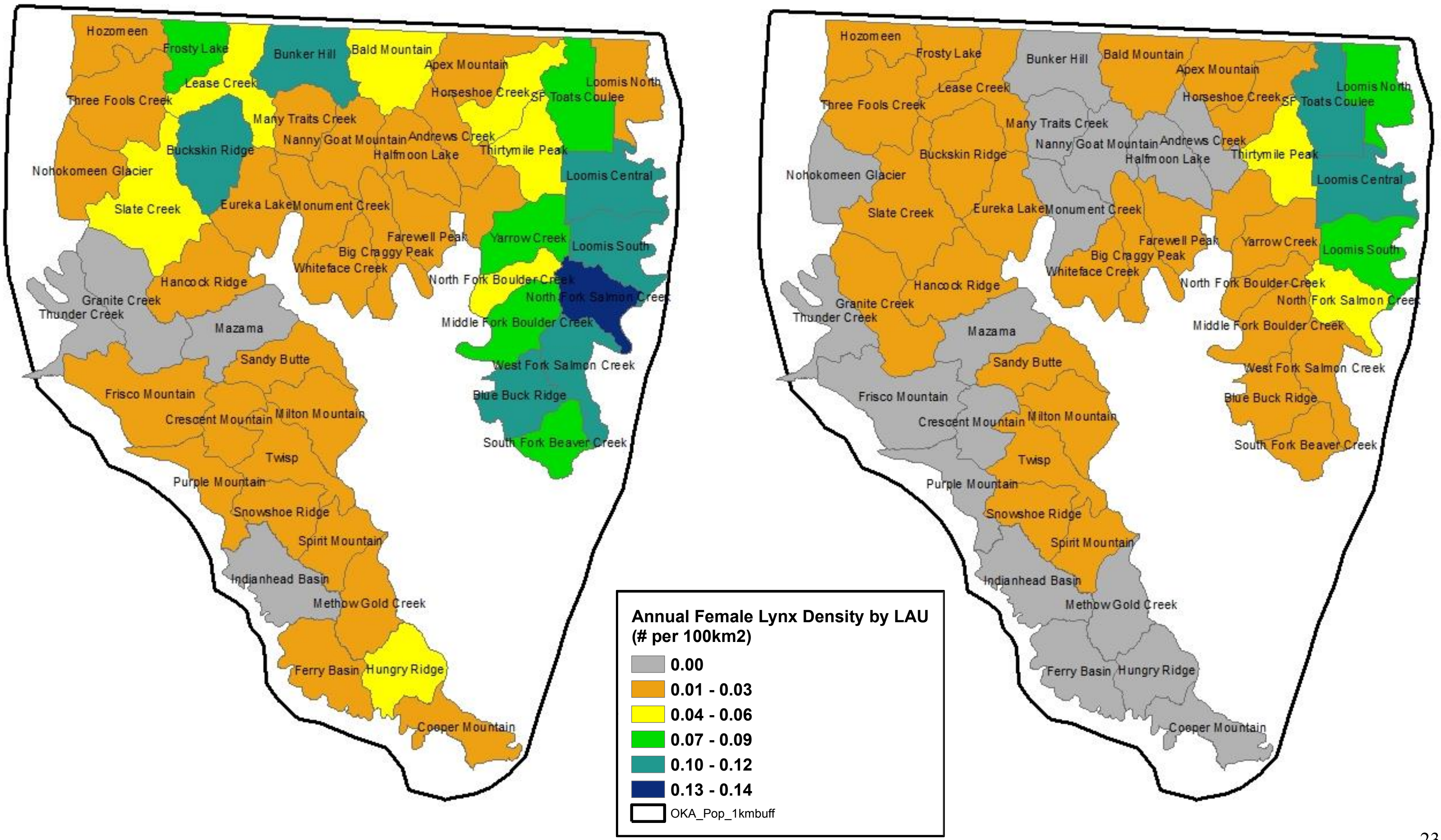


Figure 8. Spatial distribution of mean annual territorial female lynx density (# per 100km^2) by LAU in the Kettle LMZ. Differences between scenarios were a result of resource changes due to disturbance, primarily wildfire, with three different home range sizes (39km^2, 55km^2, and 72 km^2). Color scheme and range of values were held constant within each home range to show the influence of disturbance on modeled density outcomes.

Home Range: 39km^2

Scenario: 39_pre-fire

Scenario: 39_post-fire

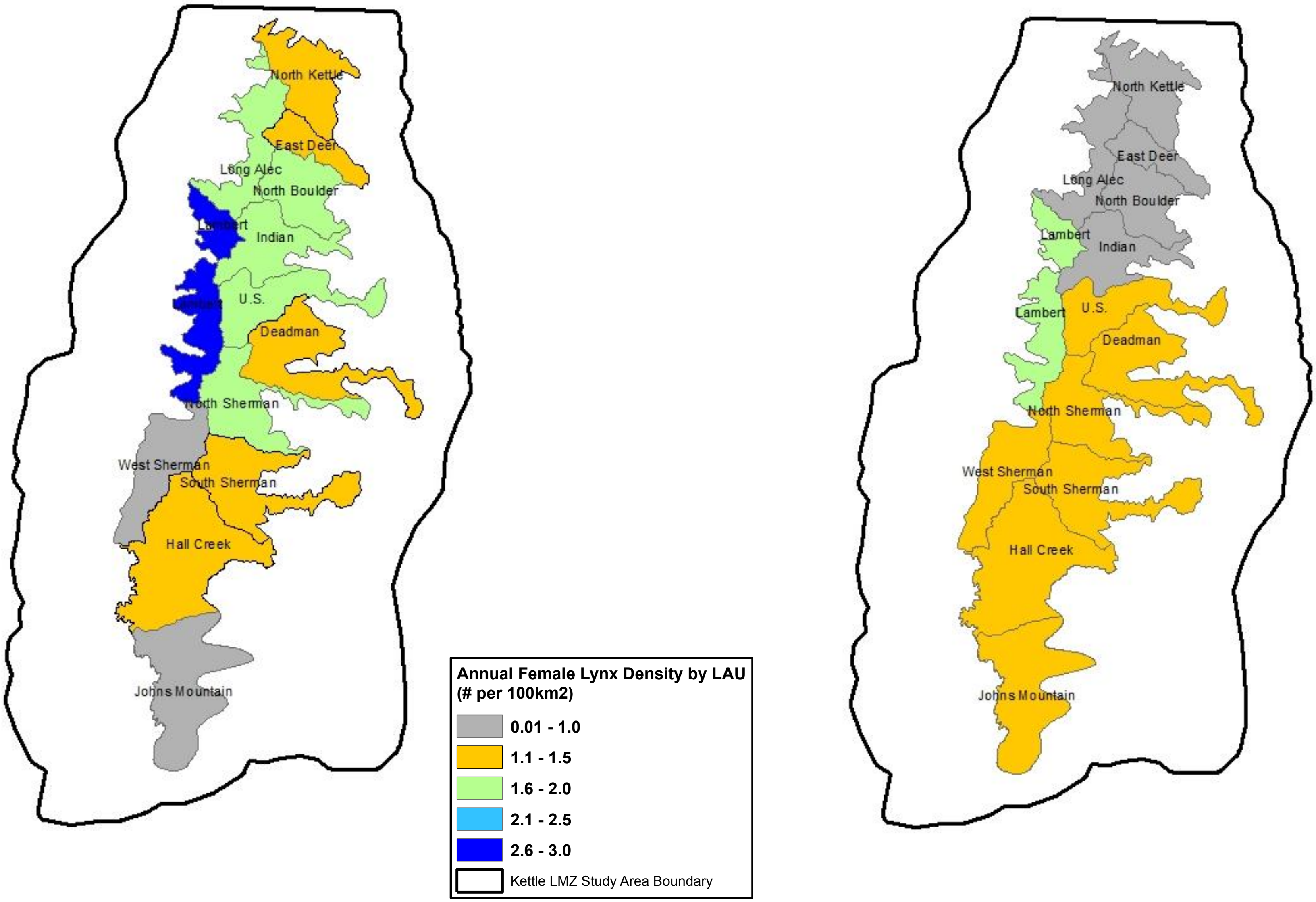


Figure 8. continued

Home Range: 55km^2

Scenario: 55_pre-fire

Scenario: 55 post-fire

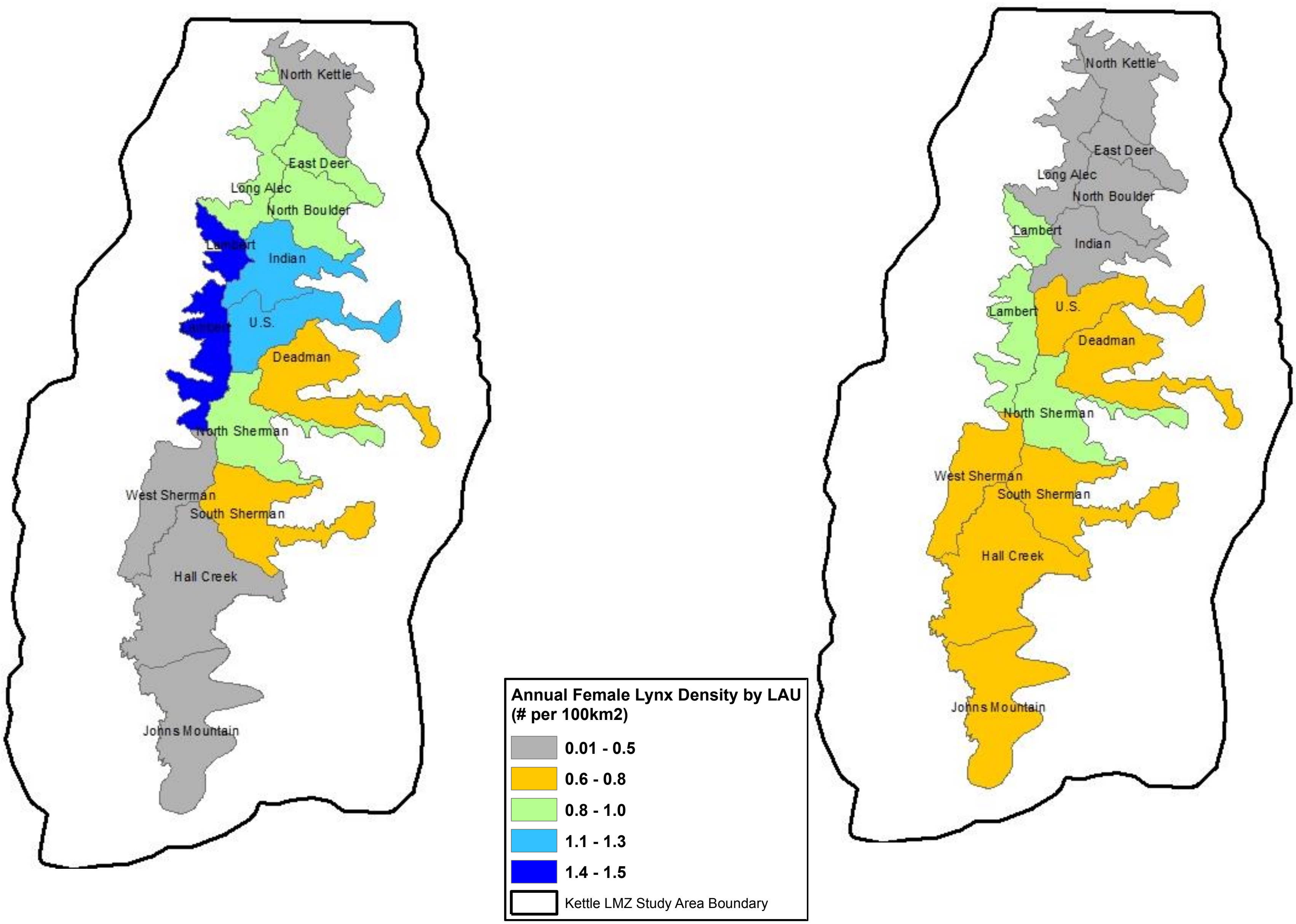
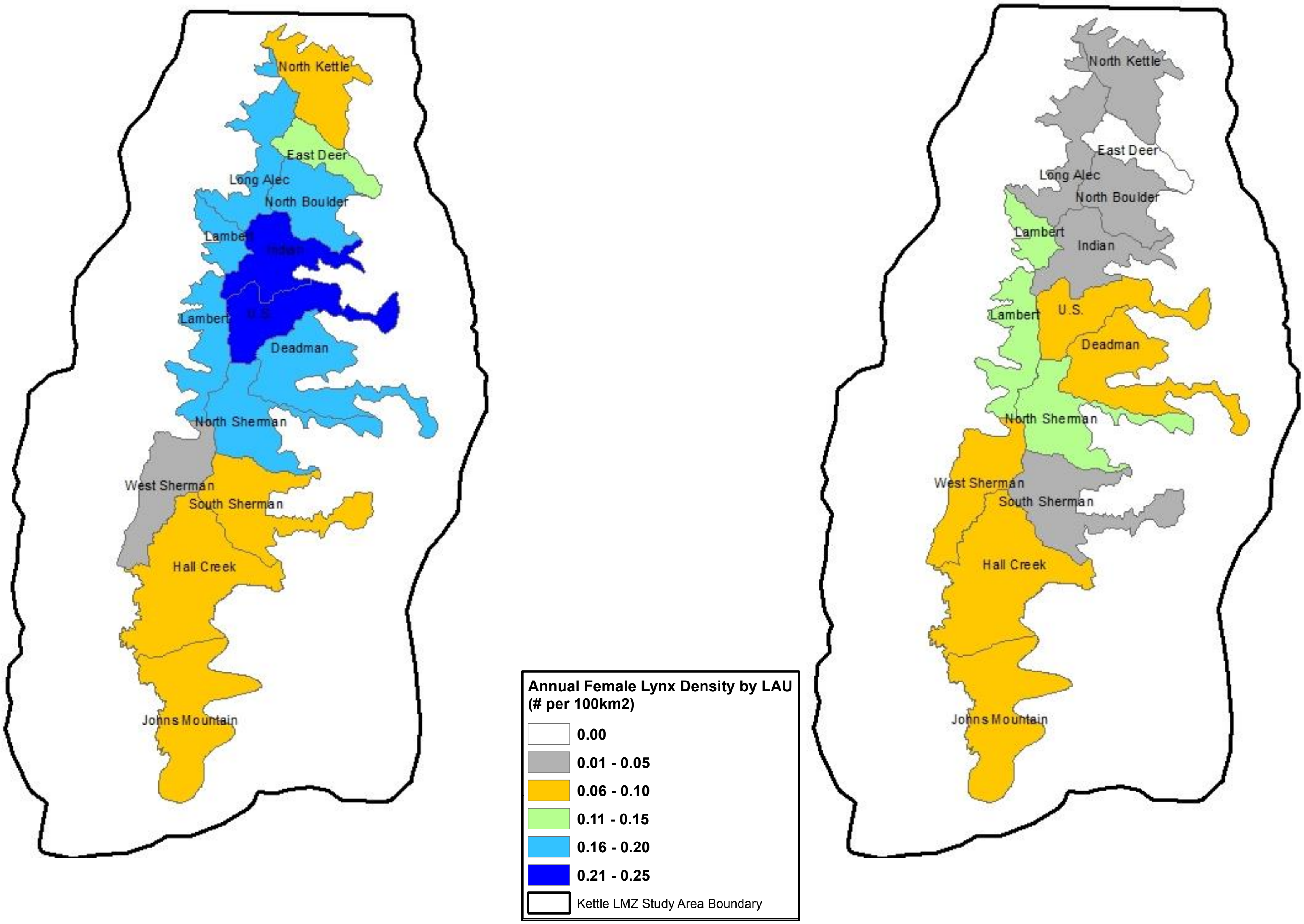


Figure 8. continued

Home Range: 72 km^2

Scenario: 72_pre-fire

Scenario: 72_post-fire



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Appendix S1. Literature sources and associated data values for demographic parameters used in the development of the Okanogan and Kettle Lynx Management Zones Canada lynx carrying capacity models.

Table S1. Summary of lynx GPS data and calculated homerange area based on 95% minimum convex polygon (calculated in R, adehabitatHR, Calenge 2006). Range and mean home range area for female and male lynx within the OLMZ was used to determine habitat composition.

ID	Sex	Dates	# locations	95% MCP (km^2)	Mean (km^2)
LF1	F	3/12-12/12	1243	106.5	
LF2	F	3/10-11/10	863	42.1	
LF3	F	3/12-8/12	745	67.3	Females: 72.0
LM1	M	2/08-12/09	1787	76.1	
LM2	M	2/12-1/13	1733	73.2	
LM3	M	2/08-1/09	1574	36.5	
LM4	M	3/12-6/13	1604	125.2	
LM5	M	3/09-10/10	1900	689.7	
LM6	M	3/11-10/11	838	231.4	
LM7	M	4/11-10/11	543	19	
LM8	M	2/09-10/09	941	118.9	
LM9	M	4/08-3/09	631	24.9	
LM10	M	2/10-11/10, 3/11-4/12	2998	106	
LM11	M	3/11-10/11	740	102.7	Males: 92.6
LM12	*M*	*2/07-3/07*	*193**	*Na*	
LM13	*M*	*1/07-2/07*	*126**	*Na*	

*Did not use in model. Too few locations.

Table S2. Sources used to determine survival estimates for NCE lynx carrying capacity models. Data was unavailable specific to yearlings so we used subadult values for yearlings in all models.

	Survival Rate by Age Class			
Location	Kittens	SubAdult	Adult	Source
Washington	0.12			Koehler 1990
Maine	0.78			Vashon et al 2012
Seely Lake, MT		0.52	0.75	Squires 2016
Purcells, MT		0.68	0.85	Squires 2016
Washington			0.83	Koehler 1990
Washington			0.89	Brittel et al 1989
Colorado			0.93	Devineau et al. 2010
Colorado			0.82	Devineau et al. 2010
Yukon			0.75	Slough and Mowatt 1996, O'Donoghue et al. 1997
Yukon			0.90	Slough and Mowatt 1996, O'Donoghue et al. 1997
NW territories			0.90	Poole 1994

Table S3. Sources used to determine fecundity estimates for NCE lynx carrying capacity models.

Litter Size	Study Area	Sample Size	Years	Source
2.24	Seeley Lake, MT	33	1999-2007	Squires 2016
2.95	Purcell Mountains, MT	22	2003 - 2007	Squires 2016
2.0	Okanogan Co, WA	4 litters, 4 litters	1980 -1987	Brittel et al. 1989, Koehler 1990
3.22	MN	9	2004-2006	Moen et al. 2008
2.25 (low hare years)	ME	NA	2006-2010	Vashon et al. 2012
2.74 (high hare years)	ME	NA	1999-2005	Vashon et al. 2012
1.75 (1-3)	MT	18	1985	Brainerd 1985
3.25 (1-5)	MT	18	1985	Brainerd 1985
3.2	NS	154	1977-1980	Parker et al. 1983
3.6	NS	154	1977-1980	Parker et al. 1983

Table S4. Lynx population density estimates from other ecosystems used in comparison with carrying capacity estimates for Okanogan and Kettle LMZs.

Location	Date of estimate	Density (lynx/100 km^2)	Source
Southern Boreal Forests			
Okanogan National Forest, Washington	1985-1987	2.3	Koehler 1990
Okanogan National Forest, Washington	1989	2	Brittell et al. 1989
Yukon	1987	2.7	Slough and Mowat 1996
NW Territories	1989-1993, population low after decline in hare numbers	3	Poole 1994