RESEARCH NOTE

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Recolonizing Gray Wolves (*Canis lupus*) in Northern California: Preliminary Analysis of Suitable Areas for Reoccupancy

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ABSTRACT: After almost a century of absence, gray wolves (*Canis lupus*) are beginning to recolonize California. Based on current knowledge of wolf habitat use, we developed an expert opinion model to explore the prospects for wolf recovery in Northern California. In our model, we consider the following variables: ungulate prey availability, forest canopy cover, human population density, road density, and livestock distribution. The resulting maps predict favorable wolf habitat and identify areas with high potential for wolf–human conflict in Northern California. Validation and refinement of our model will be possible once California-specific wolf distribution data becomes available. Until then, the preliminary findings from this study can inform management of this endangered species.

Index terms: Canis lupus, endangered species, habitat modeling, human–wildlife conflict, Northern California

INTRODUCTION

The gray wolf (*Canis lupus* L.) historically inhabited California (Paquet and Carbyn 2003) but was extirpated from the state in the 1920s (Schmidt 1991). Since 2011, gray wolves have been recolonizing California by dispersal of individuals from populations in other states (Kovacs et al. 2016). California now hosts a small gray wolf population that is protected under federal and state law. The renewed presence of wolves in California has generated a high level of public interest, especially within ranching, conservation, and hunting communities. Because wolves prey upon livestock and compete with hunters for game, wolf recolonization often comes with potential for human–wildlife conflicts (Fritts et al. 2003).

Habitat models can be a valuable tool for addressing these impending conflicts. Habitat models allow researchers to assess habitat suitability for a particular species based on that species' use of habitat in another location. Such models have been utilized in management frameworks and have proven effective at predicting wolf habitat use in different regions of the United States (Mladenoff et al. 1995; Carroll et al. 2003; Larsen and Ripple 2006; Oakleaf et al. 2006). For purposes of this study, we adopted the definition of habitat presented by Hall et al. (1997): "The resources and conditions present in an area that produce occupancy—including survival and reproduction—by a given organism." We further equated higher habitat quality with higher frequency of use by wolves.

Gray wolves are adaptable to a wide range of ecological conditions, provided sufficient prey is available and human persecution is not excessive (Boitani 2003; Paquet and Carbyn 2003). Although wolves can have a diverse diet, ungulates account for most of the prey biomass consumed (Ballard et al. 1987; Fuller et al. 1992; Fuller et al. 2003). Research into wolf population dynamics has shown that wolf numbers are positively correlated with ungulate density (Keith 1983; Fuller et al. 1992; Fuller et al. 2003). Monitoring of wolf populations has further shown that the majority of wolf mortality is human-caused, even in areas where killing of wolves is prohibited (Ballard et al. 1987; Fuller 1989; Mech 1989). Therefore, wolves require habitat that minimizes wolf–human conflicts, which typically occur when wolves occupy areas near humans and livestock (Mech 1995; Mladenoff et al. 1995; Fritts et al. 2003; Oakleaf et al. 2006). Wolves generally select areas remote from human influence, with high human population densities precluding the presence of wolf packs (Fuller et al. 1992; Mladenoff et al. 1995; Larsen and Ripple 2006; Oakleaf et al. 2006). Similarly, several studies (Thiel 1985; Fuller et al. 1992; Mladenoff et al. 1995) have found road density to be one of the most important factors in determining suitable wolf habitat. While wolves sometimes use lightly traveled roads as travel corridors, roads have been documented to negatively affect wolf populations (Fuller 1989; Thurber et al. 1994; Mladenoff et al. 1995).

Other variables found to be associated with wolf habitat use include public land ownership and vegetation cover. However, as noted by Larsen and Ripple (2006), "these characteristics may not be a requirement by wolves per se, but rather may provide

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additional security from human contact." Characterized by lower human and road densities, public lands were positively correlated to wolf habitat use in the Great Lakes and Rocky Mountain regions (Mladenoff et al. 1995; Larsen and Ripple 2006). In addition, researchers (Mladenoff et al. 1995; Larsen and Ripple 2006; Oakleaf et al. 2006) have shown that wolves prefer forested landscapes over more open and disturbed landscapes such as grasslands and agricultural areas.

In recent years, several studies (Mesler 2015; Antonelli et al. 2016; Kovacs et al. 2016) have analyzed the prospects for wolf recovery in California, each addressing different aspects of wolf habitat and dispersal. With the recent expansion of wolves into California and the historical and present-day sociopolitical difficulties associated with wolf recolonization, more research into potential habitat and conflict areas is warranted. The objective of this study is to provide an expert opinion model to (1) predict areas likely to support wolves in Northern California and (2) identify areas with high potential for wolf–human conflict. Based on previous modeling efforts and current knowledge of wolf habitat use, we included four variables in our model: ungulate prey density, road density, human population density, and forest cover. We deemed such an a priori / expert-based approach to be justified, given the absence of empirical data collected on wolves in California at this time. Validation and refinement of our model will be possible once California-specific wolf distribution data becomes available.

METHODS

Study Area

As Oregon is the most likely source of immigrating wolves, we focused on Northern California and selected Interstate 80 as the southern boundary of our study area (127,878 km^2; Figure 1). The study area is biogeographically diverse, containing nine Level III ecoregions within its boundaries (Griffith et al. 2016). The human population of the region is 3.1 million, with a mean density of 24.1 humans/km^2 and a mean road density of 1.4 km/km^2 (American Community Survey 2010–2014, U.S. Census Bureau). Public lands account for 46% (58,336 km^2) of the study area of which 72% is managed by the US Forest Service (USFS), 15% by the Bureau of

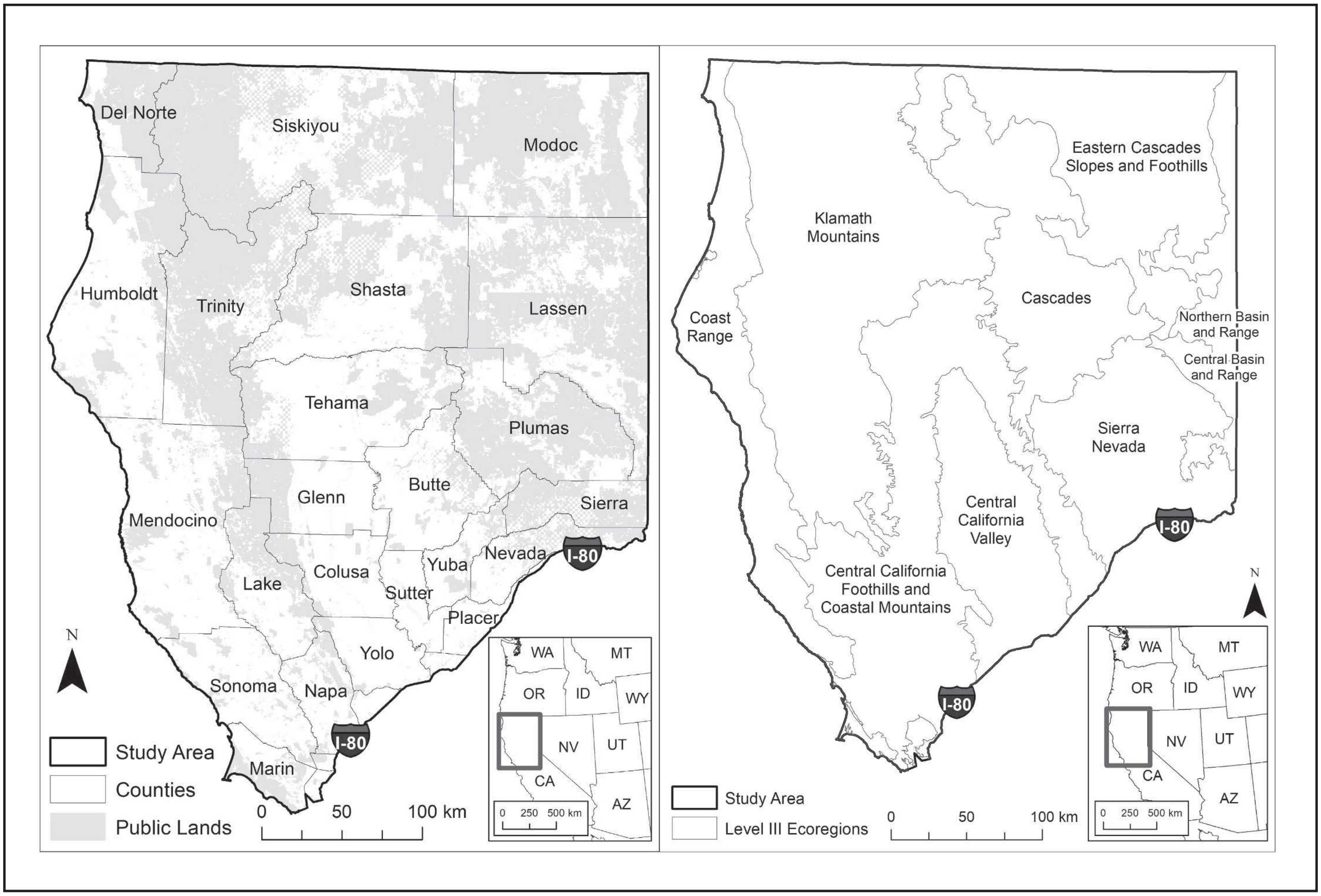

Figure 1. Study area in Northern California.

Land Management (BLM), and 10% by the National Park Service (NPS; Land Ownership, CALFIRE).

Habitat Model Development

Our model included four variables potentially important to determining suitable wolf habitat in Northern California: ungulate prey density, road density, human population density, and forest cover. Our variable selection was driven by existing habitat models that had proven effective at predicting habitat suitability for wolf populations elsewhere in the United States (Mladenoff et al. 1995; Carroll et al. 2003; Larsen and Ripple 2006; Oakleaf et al. 2006). Other variables considered but not modeled included public land ownership, land use, vegetation type, elevation, slope, distance from roads, roadless areas, impervious surfaces, and livestock density. These variables were not included due to either their perceived high correlation with other variables or their expected lack of impact (or ambiguous impact) on wolf habitat selection. In the case of livestock density, data was only available at the county level, making its use impractical for our analysis.

We used ArcGIS 10.4 (Esri, Redlands, California, USA) for model development and resampled all input layers to a common resolution (30-m cell size). A simplified flowchart depicting the sequence of spatial operations in our model is included in the Appendix (Figure A1). Because identifying favorable wolf habitat involves locating areas that (1) contain sufficient prey and (2) provide security from humans (Mladenoff et al. 1995; Larsen and Ripple 2006), we divided our model into two submodels: prey availability and human influence.

The inputs for the prey availability submodel included 2015 ungulate (deer, elk, and pronghorn) population estimates from California Department of Fish and Wildlife (CDFW). We normalized the relative biomass of deer, elk, and pronghorn by using the same Ungulate Biomass Index (UBI) as Fuller et al. (2003), resulting in a combined ungulate density layer expressed in deer-equivalent units/km^2. Our human influence submodel included three variables: human population density, road density, and forest cover. Human density was based on demographic data at the census block-group level (ACS 2010–2014, US Census Bureau). To determine road density, we applied the line density tool to road network data (TIGER/Line Shapefiles, US Census Bureau) queried to include only paved roads and improved unsurfaced roads passable by two-wheel-drive automobiles. Unimproved roads were omitted, as wolves use lightly traveled roads as travel corridors (Thurber et al. 1994). We also included forest cover (USFS Analytical Canopy Product, National Land Cover Database 2011) as part of our human influence submodel, as it provides cover for avoiding humans (Boitani 2003).

To combine the variables from the human influence submodel, we assigned each to a continuous ranking from 1 to 10, with higher values reflecting greater habitat suitability. Because animals respond to habitat features in nonlinear ways (Johnston and Graham 2016), we used nonlinear functions to transform variables into suitability values. We applied a logistic decay function to human density values, with all values $\geq$8 humans/km^2 being assigned a suitability value of 1. The selection of this function was informed by Mladenoff et al. (1995) and Larsen and Ripple (2006), who had found that (1) wolves most prefer areas that have low human density; (2) as human density increases, wolf habitat suitability rapidly decreases; and (3) areas with a human population density $\geq$8 humans/km^2 generally precluded wolf occupancy. Road density data was transformed using a logistic decay function with an upper threshold of 1 km of road/km^2 based on studies that found that wolves cease to be present when road densities exceed 0.59 to 1.0 km/km^2 (Thiel 1985; Mech 1989; Mladenoff et al. 1995). We applied a logistic growth function to the tree canopy layer, as this variable is inversely related to human influence. With all three variables assigned to a common scale, we summed overlying cell values to calculate a human influence index. To combine the two submodels, we converted the ungulate biomass and human influence indices to a common scale, which we again determined to be a continuous ranking from 1 to 10. Assigning equal weight to both models, we then added overlying cell values from the two layers together, resulting in a final habitat suitability map.

Livestock Distribution

Domestic livestock in Northern California include primarily sheep and cattle, for which we utilized population estimates at the county level (2012 Census of Agriculture). We also joined animal unit months (AUMs) data to BLM and USFS active grazing allotment boundaries to calculate AUM densities for each grazing allotment. An AUM is the amount of forage needed to feed one animal unit (the equivalent of one mature cow) for one month. It is a standard unit used to calculate the relative grazing impact of different kinds of livestock. Because BLM and USFS together own >86% of public lands in the study area (and few NPS units give out grazing permits), the AUM density layer is a nearly comprehensive indicator of livestock distribution on public lands in the region. Due to the low spatial resolution of the livestock and AUM density layers, both variables had to be excluded from our model. Until higher resolution data becomes available, our preliminary mapping efforts provide an overview and can inform future modeling.

RESULTS AND DISCUSSION

The prey availability submodel indicated that ungulate densities in Northern California were highest in the Klamath Mountains, Coast Ranges, and Sierra Nevada, while prey was least abundant in northeastern California (Figure 2). Prey densities ranged from 0.45 to 3.6 deer-equivalent units/km^2, with deer forming the vast majority of available ungulate prey. The human influence submodel showed that the study area on a landscape scale has few core areas undisturbed by humans (Figure 3). Combining prey availability and human influence variables, our model predicted that the most favorable wolf habitat is primarily concentrated in the Klamath Mountains, Coast Ranges, Cascades, and Sierra Nevada (Figure 4). The Eastern Cascades Slopes and Foothills and Central California Valley and Foothills were generally found to be unsuitable for wolf reoccupancy.

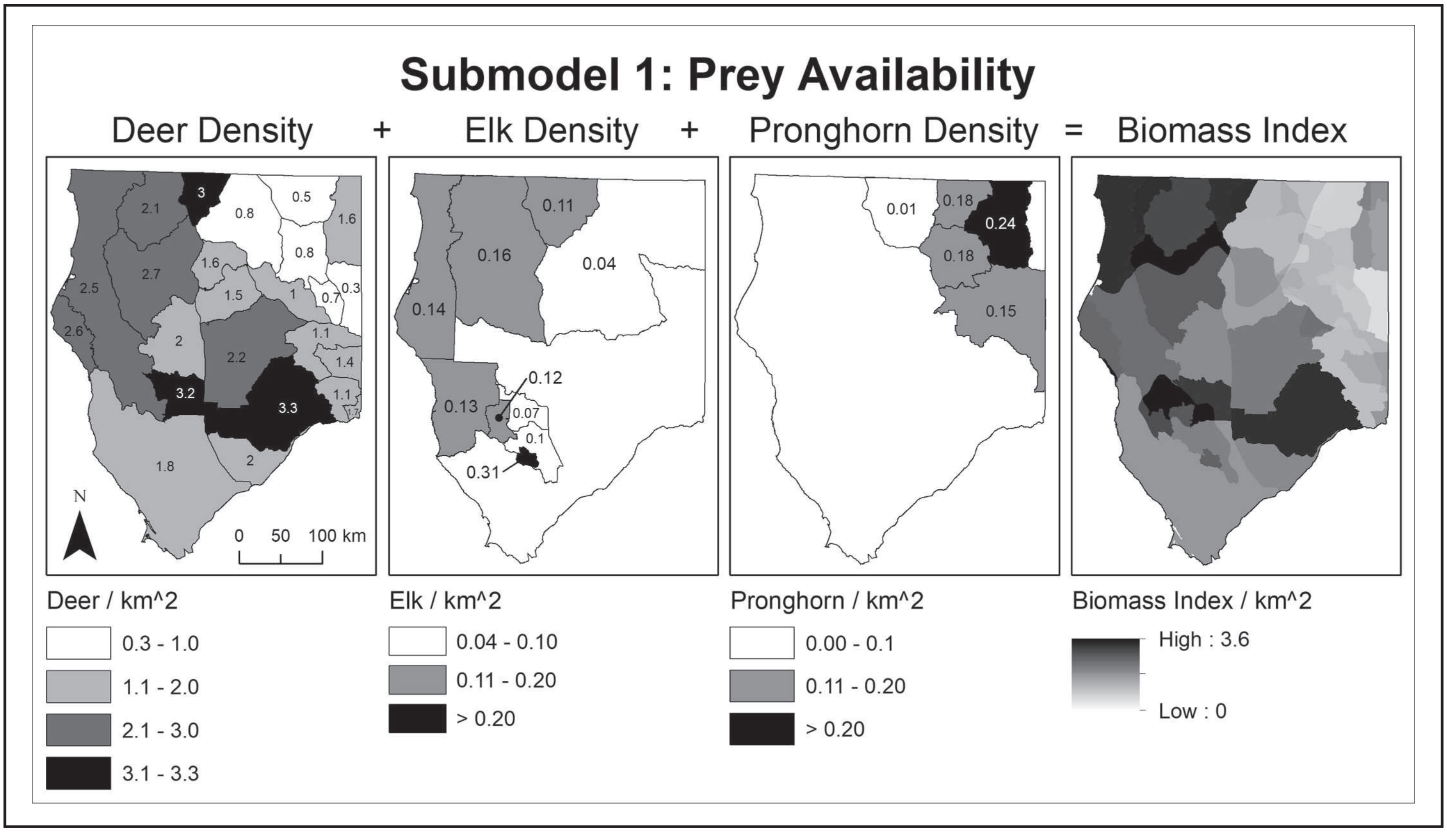

Figure 2. Inputs and output of the prey availability submodel 1. This represents the equation: deer density + elk density + pronghorn density = ungulate biomass index.

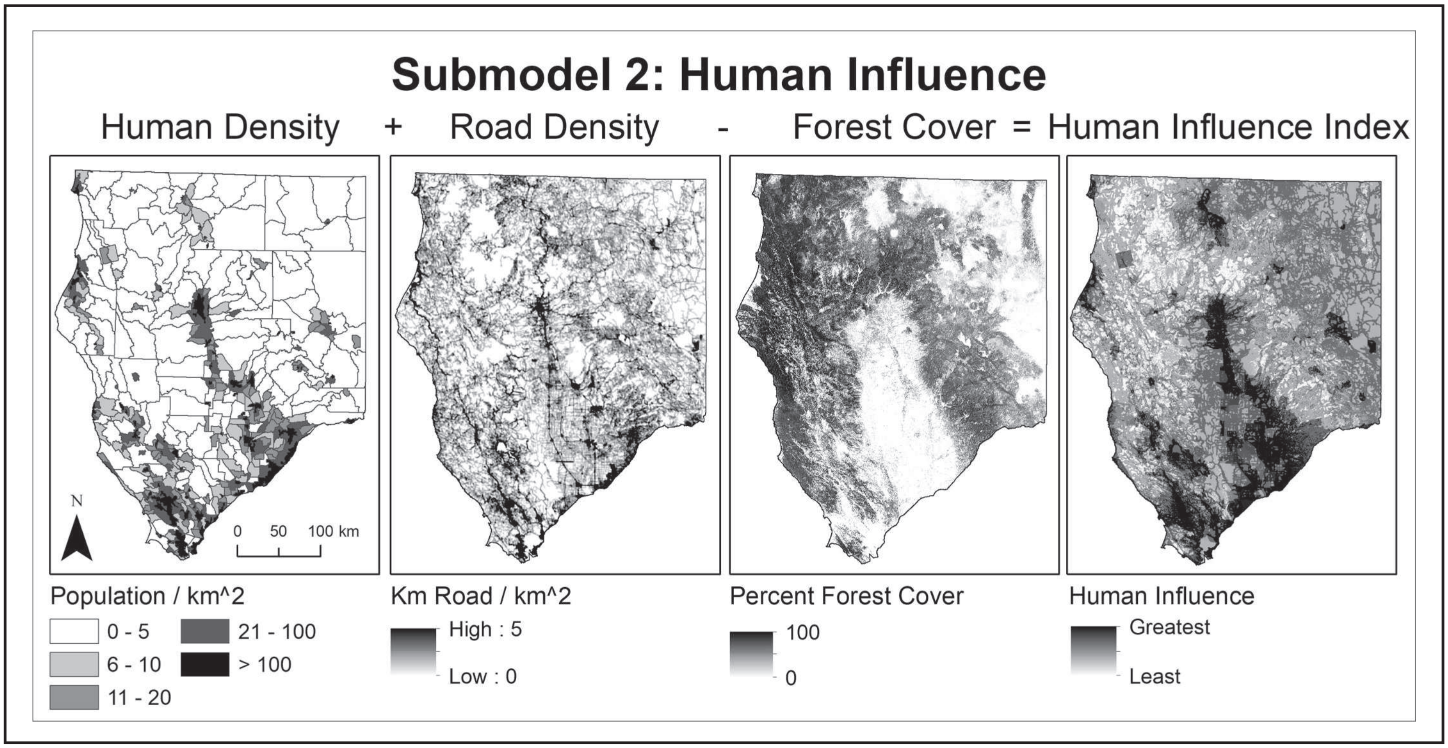

Figure 3. Inputs and output of the human influence submodel 2. This represents the equation: human population density + road density – forest cover = human influence index.

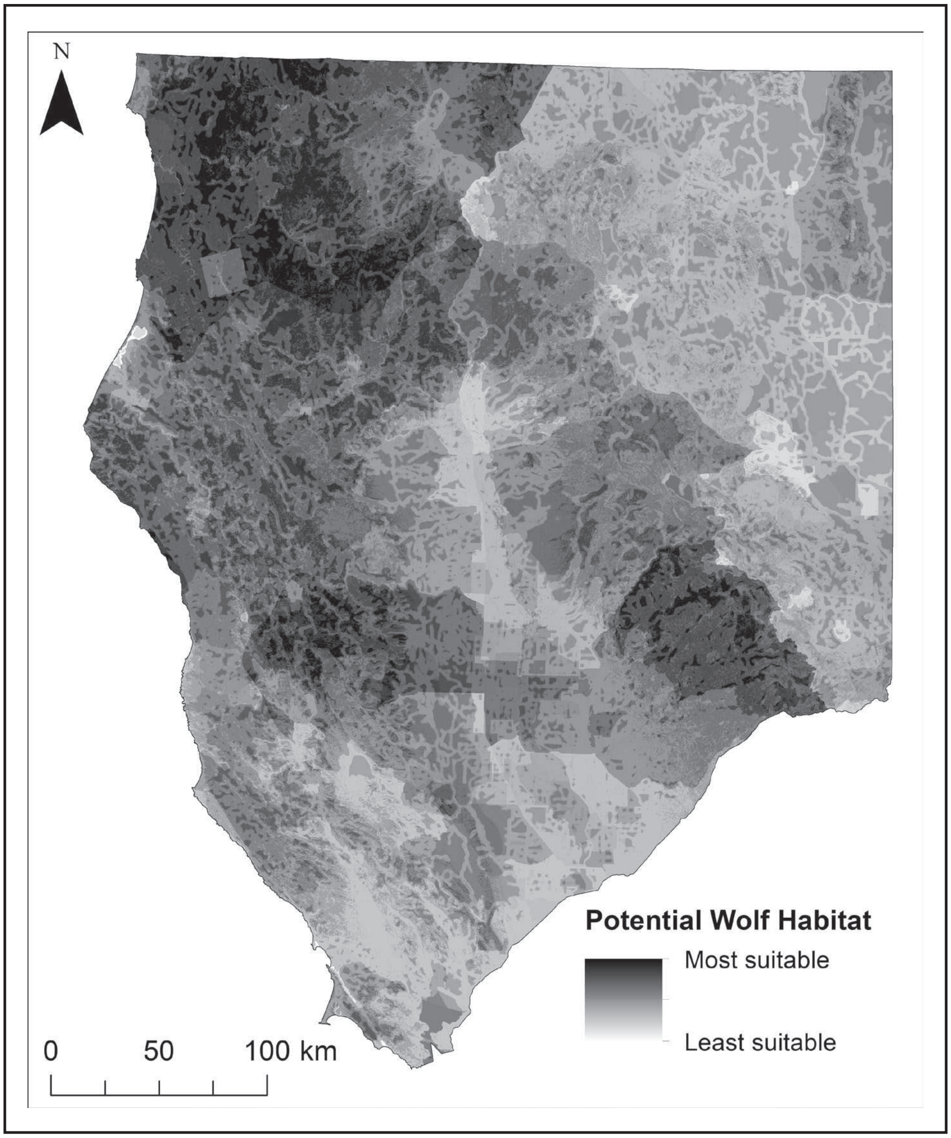

Figure 4. Habitat suitability map for wolves in Northern California.

Despite differing approaches and modeling techniques, these suitability predictions generally match those of other studies (Mesler 2015; Antonelli et al. 2016; Kovacs et al. 2016) that have modeled wolf habitat in California. Using a multivariate maximum-entropy (Maxent) model and radio-collar data from wolf packs in the Pacific Northwest, Mesler (2015) identified similar areas of high habitat quality in the northern Sierra Nevada and northwestern California. Antonelli et al. (2016) developed three models that predicted the best potential wolf habitat to include the Sierra Nevada and northwestern California. Based on the overlap of their wolf habitat suitability models with areas of known grazing in California, Antonelli et al. (2016) further predicted that northwestern California, portions of the southern Cascades, and the northern Sierra Nevada will be most prone to wolf–livestock conflicts. The CDFW's Wolf Conservation Plan (Kovacs et al. 2016) combined simplified versions of the Carroll et al. (2006), Larson and Ripple (2006), and Oakleaf et al. (2006) approaches to identify areas where wolves may become established in California. In contrast to other models, CDFW predicted that a large portion of the Eastern Cascade Slopes and Foothills would support wolf reoccupation. Because this region has a high density of grazing allotments (Figure 5), CDFW anticipates that wolf–livestock conflicts will be more frequent in the Eastern Cascade Slopes and Foothills than elsewhere in Northern California, contradicting the wolf–livestock conflict risk mapping by Antonelli et al. (2016). Whether this region proves favorable for wolf reoccupancy is consequential for the future management of this species in California.

The diverging outcomes of existing models illustrates the uncertainties involved in predicting habitat in a region that is only recently being recolonized by wolves. Absent human influence, wolves can persist under a wide range of conditions, and extrapolating results from other study areas may lead to inaccurate predictions and false inferences. Currently, all models predicting wolf habitat in California rely on studies conducted elsewhere and, as such, require validation and improvement. Mesler (2015) relied on wolf presence data collected in Oregon and Washington, Antonelli et al. (2016) utilized wolf data from Oregon, and Kovacs et al. (2016) combined approaches that had been developed based on wolf habitat use in the Northern Rocky Mountains. Similarly, the model developed in this study was informed by research carried out in the Rocky Mountains, Pacific Northwest, and Great Lakes regions. Thus, this preliminary study identifies areas where wolves could potentially thrive in Northern California for the given scenario. Many more potential scenarios exist. The lack of tracking data, an insufficient number of wolves, and too short of a timeframe limit robust spatial- and temporal-scale research at the moment. More accurate habitat predictions will be possible once California-specific wolf distribution data become available. To this end, it will be critical to closely monitor current wolf populations in California and Oregon by employing a variety of surveying methods, including telemetry, track/scat/hair deposit surveys, howling surveys, and remote camera surveys. Until then, it will be important to estimate where wolves are most likely to reestablish, and existing wolf habitat models can be a helpful starting point in identifying those areas. Our preliminary research is one step in understanding the possible outcomes of the given combination of variables involved.

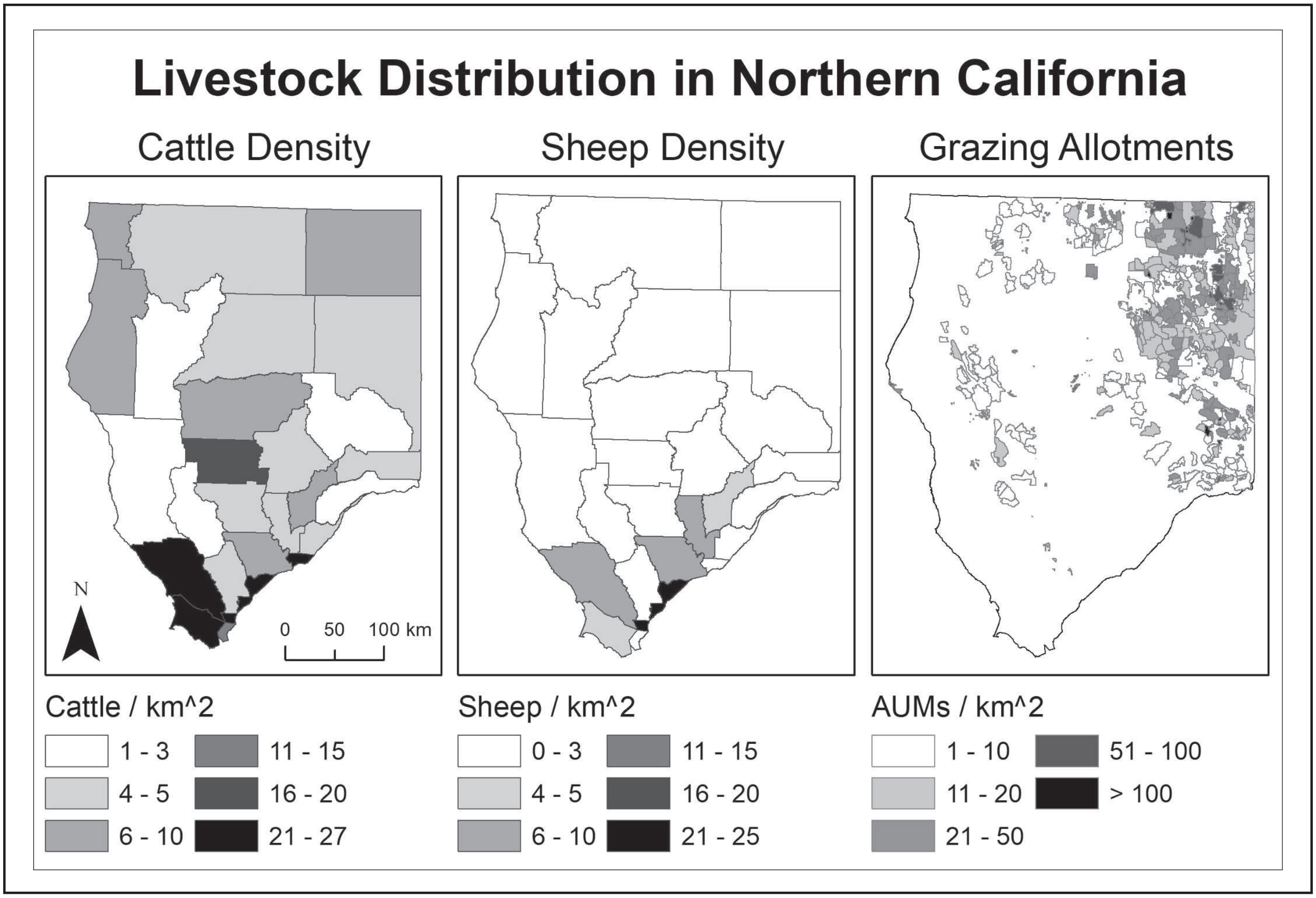

Figure 5. Livestock distribution in Northern California.

NOTE: Refer to BioOne online for Supplementary Figure A1, flowchart depicting the sequence of spatial operations in our model.

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Tobias Nickel holds a BA in environmental studies, political science, and philosophy from the University of San Diego. He has worked for the National Park Service, the Bureau of Land Management, the California Wolf Center, and the Catalina Island Conservancy. Currently, Tobias is a Wilderness Ranger with the US Forest Service in New Mexico. Beginning in the fall, he will be studying toward a Master's in Public Land Management at Western Colorado University.

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