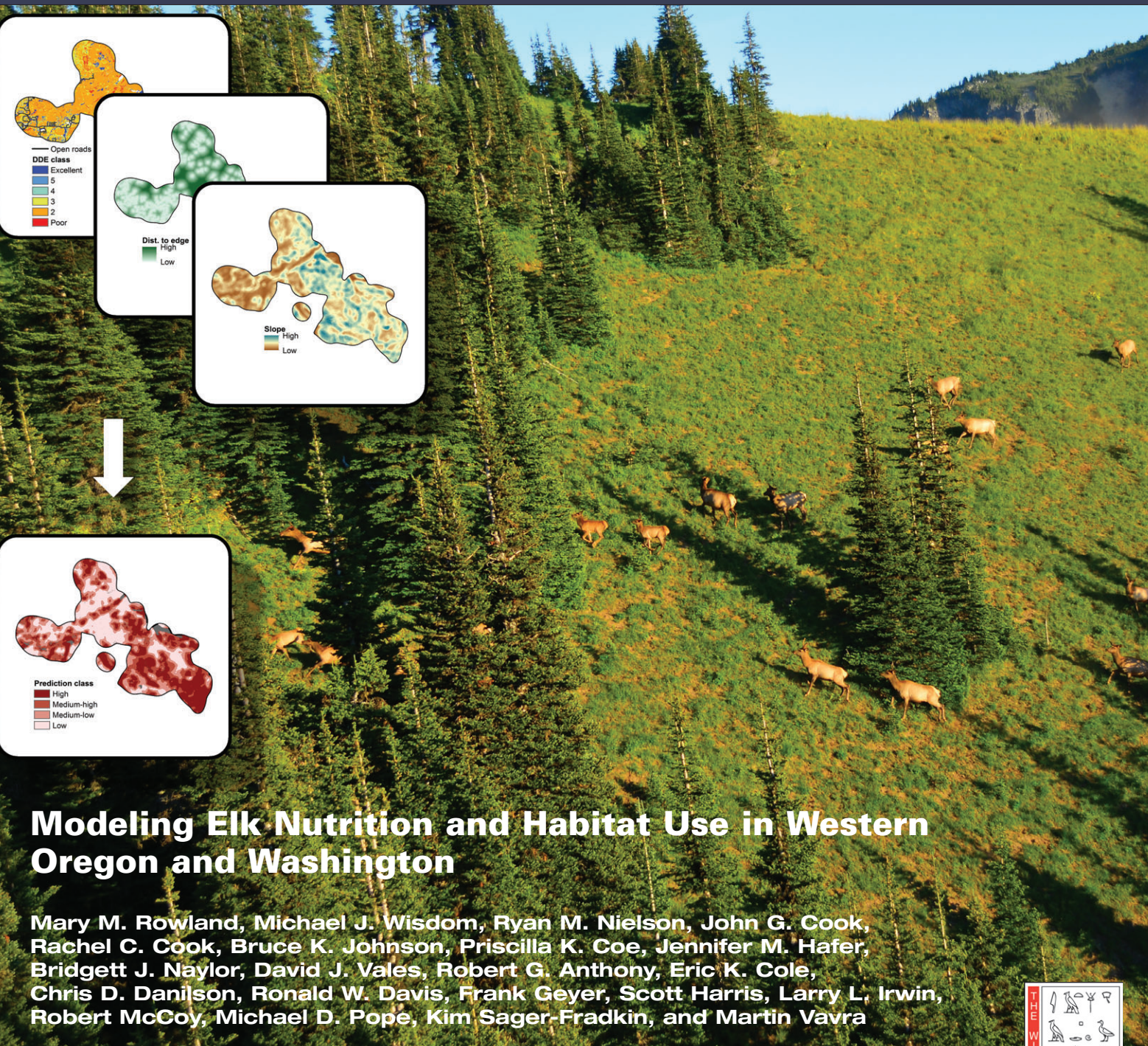


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Modeling Elk Nutrition and Habitat Use in Western Oregon and Washington

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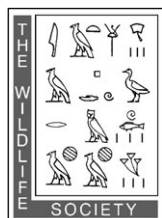
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Cover Image: Understanding nutritional resources and habitat use of large herbivores like elk (*Cervus canadensis*) can benefit their management across multiple land ownerships and management regimes. Dietary digestible energy, distance to open roads, distance to cover-forage edge, and slope were the best predictors of habitat use by elk during summer in a landscape model developed for western Oregon and Washington. Photo by Michael P. Middleton, Muckleshoot Indian Tribe.



Rocky Mountain elk (*Cervus canadensis*) in the Green River drainage, Washington, are likely descendants from Yellowstone transplants in the early 1900s. Elk in this region provided much of the telemetry data used in modeling elk habitat use in the Westside region. Photo by Michael P. Middleton, Muckleshoot Indian Tribe.



Modeling Elk Nutrition and Habitat Use in Western Oregon and Washington

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ABSTRACT Studies of habitat selection and use by wildlife, especially large herbivores, are foundational for understanding their ecology and management, especially if predictors of use represent habitat requirements that can be related to demography or fitness. Many ungulate species serve societal needs as game animals or subsistence foods, and also can affect native vegetation and agricultural crops because of their large body size, diet choices, and widespread distributions. Understanding nutritional resources and habitat use of large herbivores like elk (*Cervus canadensis*) can benefit their management across different land ownerships and management regimes. Distributions of elk in much of the western United States have shifted from public to private lands, leading to reduced hunting and viewing opportunities on the former and increased crop damage and other undesired effects on the latter. These shifts may be caused by increasing human disturbance (e.g., roads and traffic) and declines of early-seral vegetation, which provides abundant forage for elk and other wildlife on public lands. Managers can benefit from tools that predict how nutritional resources, other environmental characteristics, elk productivity and performance, and elk distributions respond to management actions. We present a large-scale effort to develop regional elk nutrition and habitat-use models for summer ranges spanning 11 million ha in western Oregon and Washington, USA (hereafter Westside). We chose summer because nutritional limitations on elk condition (e.g., body fat levels) and reproduction in this season are evident across much of the western United States. Our overarching hypothesis was that elk habitat use during summer is driven by a suite of interacting covariates related to energy balance: acquisition (e.g., nutritional resources, juxtaposition of cover and foraging areas), and loss (e.g., proximity to open roads, topography). We predicted that female elk consistently select areas of higher summer nutrition, resulting in better animal performance in more nutritionally rich landscapes. We also predicted that factors of human disturbance, vegetation, and topography would affect elk use of landscapes and available nutrition during summer, and specifically predicted that elk would avoid open roads and areas far from cover-forage edges because of their preference for foraging sites with secure patches of cover nearby. Our work had 2 primary objectives: 1) to develop and evaluate a nutrition model that estimates regional nutritional conditions for elk on summer ranges, using predictors that reflect elk nutritional ecology; and 2) to develop a summer habitat-use model that integrates

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the nutrition model predictions with other covariates to estimate relative probability of use by elk, accounting for ecological processes that drive use. To meet our objectives, we used 25 previously collected data sets on elk nutrition, performance, and distributions from 12 study areas. We demonstrated the management utility of our regional-scale models via application in 2 landscapes in Washington.

The elk nutrition model predicts levels of digestible energy in elk diets (DDE; kcal DE/g of consumed forage) during summer. Model input data were from foraging experiments using captive female elk and field measurements of site characteristics at fine scales (~ 0.5 ha). The nutrition model included a set of equations that predicted forage biomass as a function of site characteristics and a second set that predicted DDE primarily as a function of forage biomass. We used the nutrition model to develop a DDE map across the Westside. We then evaluated performance of the model by comparing predicted DDE to nutritional resource selection by elk and to population-level estimates of autumn body fat and pregnancy rates of lactating elk. To model elk habitat use, we compiled 13 unique telemetry data sets from female elk ($n = 173$) in 7 study areas (data collected June–August 1991–2009). We used a generalized linear model with 5 of the data sets, coupled with ecologically relevant covariates characterizing nutrition, human disturbance, vegetation, and physical conditions, to estimate intensity of use with the negative binomial model. We evaluated model performance by mapping predicted habitat use with the regional model and comparing predictions with counts of elk locations using 8 independent telemetry data sets.

The nutrition model explained a reasonably high amount of variation in forage biomass ($r^2 = 0.46$ – 0.72) and included covariates of overstory canopy cover, proportion of hardwoods in the canopy, potential natural vegetation (PNV) zone, and study area. Dietary DE equations in the model explained about 50% of the variation in DDE ($r^2 = 0.39$ – 0.57) as a function of forage biomass by PNV zone and study area. Broad-scale application of the nutrition model in the Westside region illustrated the predominance of landscapes that failed to meet nutritional needs of lactating females (≤ 2.58 kcal/g) and their calves, especially at moderate elevations in closed-canopy forests in both the Coast Range and the southern Cascades. Areas providing DDE at (> 2.58 – 2.75 kcal/g) or in excess (> 2.75 kcal/g) of the basic requirement of lactating females were uncommon ($< 15\%$ of area) or rare ($< 5\%$ of area), respectively, and primarily occurred in early-seral communities, particularly at higher elevations. Wild elk avoided areas with DDE below basic requirement and selected for areas with DDE > 2.60 kcal/g. Percentage of elk ranges providing DDE levels near or above basic requirement was highly correlated with pregnancy rates of lactating females. Autumn body fat levels were highly correlated with percentage of elk ranges providing DDE levels above basic requirement.

The regional model of elk habitat use with greatest support in the empirical data included 4 covariates: DDE, distance to nearest road open to motorized use by the public, distance to cover-forage edge, and slope. Elk preferred habitats that were relatively high in DDE, far from roads, close to cover-forage edges, and on gentle slopes. Based on standardized coefficients, changes in slope (-0.949) were most important in predicting habitat use, followed by DDE (0.656), distance to edge (-0.305), and distance to open road (0.300). Use ratios for the regional model indicated these changes in relative probability of use by elk: a 111.2% increase in use for each 0.1-unit increase in DDE; a 22.7% increase in use for each kilometer away from an open road; an 8.1% decrease in use for each 100-m increase in distance to edge; and a 5.3% decrease in use for each percent increase in slope. The regional model validated well overall, with high correlation between predicted use and observed values for the 4 Washington sites ($r_s \geq 0.96$) but lower correlation in southwestern Oregon sites ($r_s = 0.32$ – 0.87).

Our results demonstrated that nutrition data collected at fine scales with captive elk can be used to predict nutritional resources at large scales, and that these predictions directly relate to habitat use and performance of free-ranging elk across the Westside region. These results also highlight the importance of including summer nutrition in habitat evaluation and landscape planning for Westside elk. The models can inform management strategies to achieve objectives for elk across land ownerships. The regional model provides a useful tool to understand and document spatially explicit habitat requirements and distributions of elk in current or future landscapes. The 2 examples of management application demonstrated how effects of management on elk nutrition and habitat use can be evaluated at landscape scales, and in turn how animal performance and distribution are affected. Results further illustrated the importance of managing for nutrition in combination with other covariates (i.e., roads, slope, cover-forage edges) that affect elk use of nutritional resources to achieve desired distributions of elk. Our meta-analysis approach to habitat modeling provides a useful framework for research and management of wildlife species with coarse-scale habitat requirements by identifying commonalities in habitat-use patterns that are robust across multiple modeling areas and a large geographic range. Use of such methods in future modeling, including application in monitoring programs and adaptive management, will continue to advance ecological knowledge and management of wildlife species like elk. © 2018 The Authors. Wildlife Monographs published by Wiley on behalf of The Wildlife Society. This is an open access article under the terms of the Creative Commons Attribution-NonCommercial-NoDerivs License, which permits use and distribution in any medium, provided the original work is properly cited, the use is non-commercial and no modifications or adaptations are made.

KEY WORDS animal performance, *Cervus canadensis*, elk, habitat-use model, land management, meta-analysis, nutritional ecology, Pacific Northwest.

Modelando la Nutrición de Alce y el Uso del Hábitat en el Oeste de Oregon y Washington

RESUMEN Los estudios de selección y uso de hábitats por la vida silvestre, especialmente herbívoros grandes, son fundamentales para comprender su ecología y gestión, especialmente si los predictores de uso representan requisitos de hábitat que pueden estar relacionados con la demografía o aptitud física. Muchas especies de ungulados sirven a las necesidades de la sociedad como animales de caza o alimento sustancial, y también pueden afectar la vegetación nativa y los cultivos agrícolas debido a sus grandes opciones de dieta de tamaño corporal y su amplia distribución. El entendimiento de los recursos nutricionales y el uso de hábitat de grandes herbívoros como el alce (*Cervus canadensis*) puede beneficiar su gestión en diferentes propiedades de la tierra y regímenes de gestión. Distribuciones de alce en gran parte del oeste de los Estados Unidos han cambiado de tierras públicas a privadas, conduciendo a oportunidades a la caza y observación reducidas en la primera y el aumento del daño a los cultivos y otros efectos no deseados en este último. Estos cambios pueden ser causados por el aumento de la perturbación humana (por ejemplo, carreteras y tráfico) y la disminución de la vegetación seral-temprana, que proporcionan abundante forraje para los alces y otros animales salvajes en las tierras públicas. Los gerentes pueden beneficiarse de técnicas que predicen cómo los recursos nutricionales, otras características ambientales, la productividad y el rendimiento de los alces y las distribuciones de alces responden a las acciones de la administración. Presentamos un esfuerzo a gran escala para desarrollar modelos regional de nutrición de alces y uso de hábitats para las zonas de distribución de verano que abarcan 11 millones de hectáreas en el oeste de Oregon y Washington, EE. UU. (en lo sucesivo Westside). Elegimos verano porque limitaciones nutricionales a condición del alce (por ejemplo, niveles de grasa corporal) y la reproducción en esta temporada son evidentes en gran parte de los Estados Unidos. Nuestra hipótesis general era que el uso de hábitat de alces durante el verano está impulsado por un conjunto de covariables que interactúan relacionadas con el equilibrio energético: adquisición (por ejemplo, recursos nutricionales, yuxtaposición de áreas de cobertura y áreas de forrajeo) y pérdida (por ejemplo, proximidad a caminos abiertos, topografía). Predijimos que las alces hembra seleccionan consistentemente áreas de mayor nutrición de verano, lo que resulta en un mejor rendimiento animal en paisajes más ricos nutricionalmente. También predijimos que los factores de perturbación humana, vegetación y topografía afectarían el uso de alces de los paisajes y la nutrición disponible durante el verano, y predijimos específicamente que el alce evitaría caminos abiertos y áreas lejos de los bordes de forraje debido a su preferencia por los sitios de forrajeo con parches seguros de cobertura cerca. Nuestro trabajo tuvo dos objetivos principales: 1) desarrollar y evaluar un modelo de nutrición que estima las condiciones nutricionales regionales para el alce en las zonas de distribución de verano, utilizando predictores que reflejan la ecología nutricional de los alces; y 2) desarrollar un modelo de verano de uso del hábitat que integre las predicciones del modelo de nutrición con otras covariables para estimar la probabilidad relativa de uso de alces, teniendo en cuenta los procesos ecológicos que impulsan el uso. Para cumplir nuestros objetivos, utilizamos 25 conjuntos de datos recopilados previamente sobre nutrición, rendimiento y distribuciones de alces de 12 áreas de estudio. Demostramos la utilidad de gestión de nuestros modelos a escala regional a través de la aplicación en 2 paisajes en Washington.

El modelo de nutrición de alces predice niveles de energía digestible en las dietas de alces (DDE; kcal DE/g de forraje consumido) durante el verano. Los datos de entrada del modelo provenían de experimentos de forrajeo utilizando alces femeninos cautivos y mediciones de campo de las características del sitio a escalas finas (~ 0.5 ha). El modelo de nutrición incluyó un conjunto de ecuaciones que predijeron la biomasa del forraje como una función de las características del sitio y un segundo conjunto que predijo DDE principalmente como una función de la biomasa del forraje. Usamos el modelo de nutrición para desarrollar un mapa DDE a través del Westside. Luego evaluamos el desempeño del modelo comparando DDE predicho con la selección de recursos nutricionales por alces y con las estimaciones a nivel poblacional de la grasa corporal otoñal y las tasas de embarazo de alces lactantes. Para modelar el uso del hábitat de alces, compilamos 13 conjuntos únicos de datos de telemetría de alces hembra ($n = 173$) en 7 áreas de estudio (datos recogidos en Junio – Agosto de 1991 – 2009). Utilizamos un modelo lineal generalizado con 5 de los conjuntos de datos, junto con covariables ecológicamente relevantes que caracterizan la nutrición, la perturbación humana, la vegetación y las condiciones físicas, para estimar la intensidad de uso con el modelo binomial negativo. Evaluamos el rendimiento del modelo mapeando el uso previsto del hábitat con el modelo regional y comparando las predicciones con los recuentos de las ubicaciones de los alces utilizando 8 conjuntos independientes de datos de telemetría.

El modelo de nutrición explicó una cantidad razonablemente alta de variación en la biomasa de forraje ($r^2 = 0.46\text{--}0.72$) e incluyó covariables de la cubierta del dosel, la proporción de maderas duras en el dosel, la zona de vegetación natural potencial (PNV) y el área de estudio. Dietética DE ecuaciones en el modelo explican aproximadamente el 50% de la variación en DDE ($r^2 = 0.39\text{--}0.57$) como una función de la biomasa de forraje por zona PNV y área de estudio. Aplicación a gran escala del modelo de la nutrición en la región Westside ilustró el predominio de los paisajes que no cumplió con las necesidades nutricionales de hembras lactantes (≤ 2.58 kcal/g) y

sus terneros, especialmente en elevaciones moderadas en los bosques de dosel cerrado tanto en el Coast Range y el sur de Cascades. Áreas que proporcionan DDE al (>2.58 – 2.75 kcal/g) o en exceso (>2.75 kcal/g) del requisito básico de hembras lactantes eran poco frecuentes ($<15\%$ de área) o raras ($<5\%$ de área), respectivamente, y ocurrió principalmente en las comunidades serales tempranas, particularmente en las elevaciones más altas. Alces salvajes evitadas áreas con DDE por debajo del requisito básico y se seleccionó para áreas con DDE >2.6 0 kcal/g. El porcentaje de rangos de alces que proporcionan niveles de DDE cercanos o superiores a los requisitos básicos estuvo altamente correlacionado con las tasas de embarazo de las hembras lactantes. Los niveles de grasa corporal en otoño estuvieron altamente correlacionados con el porcentaje de rangos de alces que proporcionan niveles de DDE por encima del requisito básico.

El modelo regional de uso de hábitat de alces con mayor apoyo en los datos empíricos incluyó 4 covariables: DDE, distancia a la carretera más cercana abierta al uso motorizado por el público, distancia al borde cubierta-forraje y pendiente. Alce prefirió hábitats que eran relativamente altos en DDE, lejos de las carreteras, cerca de los bordes del forraje de cobertura y en pendientes suaves. Basado en los coeficientes estandarizados, los cambios en la pendiente (-0.949) fueron los más importantes para predecir el uso del hábitat, seguidos por DDE (0.656), distancia al borde (-0.305) y distancia al camino abierto (0.300). Las relaciones utilizadas para los modelos regionales indicaron estos cambios en la relativa probabilidad de uso por alce: un aumento del 111.2% en el uso para cada 0.1 -unidad de aumento en DDE; un aumento del 22.7% en el uso por cada kilómetro de distancia de una carretera abierta; una disminución 8.1% en el uso de cada 100 -m aumento de la distancia hasta el borde; y una disminución del 5.3% en el uso para cada incremento porcentual en la pendiente. El modelo regional se validó bien en general, con una alta correlación entre el uso previsto y los valores observados para los 4 sitios de Washington ($r_s \geq 0.96$) pero una correlación más baja en los sitios del suroeste de Oregón ($r_s = 0.32$ – 0.87).

Nuestros resultados demuestran que datos de nutrición recopilados en escalas finas recogida en escalas finas con alces en cautividad puede ser utilizado para predecir los recursos nutricionales a grandes escalas, y que estas predicciones se relacionan directamente con el uso del hábitat y el rendimiento de los alces que pasan libremente en toda la región Westside. Estos resultados también destacan la importancia de incluir la nutrición de verano en la evaluación del hábitat y la planificación del paisaje para alces en el Westside. Los modelos pueden informar estrategias de gestión para alcanzar objetivos para alces en todas las propiedades de la tierra. El modelo regional proporciona una técnica útil para comprender y documentar espacialmente requisitos explícitos de hábitat y distribuciones de alces en paisajes actuales o futuros. Los 2 ejemplos de aplicación de gestión demostraron cómo los efectos del gestión sobre la nutrición de alces y el uso del hábitat pueden evaluar a escala de paisaje y, a su vez, cómo se afectan el rendimiento y la distribución del animal. Los resultados ilustran además la importancia de la gestión de la nutrición en combinación con otras covariables (es decir; carreteras, pendiente, la cobertura de los bordes del forraje) que afectan el uso de los recursos nutricionales de alces para lograr la distribución deseada de alces. Nuestro enfoque de metanálisis para el modelado de hábitats proporciona un marco útil para la investigación y el gestión de especies silvestres con requisitos de hábitats de escala gruesa al identificando elementos comunes en los patrones de uso del hábitat que son sólidos en múltiples áreas de modelado y un amplio rango geográfico. El uso de tales métodos en modelos futuros, incluida la aplicación en programas de monitoreo y gestión adaptativo, continuará avanzando el conocimiento ecológico y el gestión de especies silvestres como el alce.

Modélisation de L'alimentation du Wapiti et de son Utilisation de L'habitat dans L'ouest des États de l'Oregon et de Washington

RÉSUMÉ Les études sur la sélection et l'utilisation d'un habitat par un animal sauvage, en particulier les grands herbivores, sont cruciales pour comprendre son écologie et sa gestion, surtout si les prédicteurs de l'utilisation de l'habitat représentent des besoins qui peuvent être reliés à la démographie ou à l'état de santé de l'animal. De nombreux ongulés comblent des besoins sociétaux en tant que gibier ou nourriture de subsistance, et peuvent aussi avoir un effet négatif sur la végétation indigène et les cultures agricoles en raison de leur grande taille, de leurs choix alimentaires et de leur aire de répartition étendue. Comprendre le type de ressources nutritionnelles disponibles aux grands herbivores tels que le wapiti (*Cervus canadensis*) et l'utilisation de leur habitat peut faciliter leur gestion sous des régimes de gestion différents et sur des terres boisées ayant des propriétaires différents. Dans la plupart des régions de l'ouest des États-Unis, l'aire de répartition du wapiti a migré des terres publiques vers des terres privées, ce qui a réduit les possibilités de chasse et d'observations sur les terres publiques et accru les dommages aux récoltes et d'autres effets indésirables sur les terres privées. Il est possible que ce déplacement soit le résultat de perturbations humaines accrues (p. ex. chemins et trafic) et du déclin de la végétation dans les forêts aux premiers stades de

succession écologique qui offrent un fourrage abondant aux wapitis et autres animaux sauvages sur les terres publiques. Les outils qui prédisent la réponse des ressources nutritionnelles et d'autres caractéristiques environnementales ainsi que la productivité et la performance du wapiti et sa répartition suite à l'implantation de mesures de gestion peuvent aider les gestionnaires. Nous présentons un travail réalisé à grande échelle qui avait pour but de développer des modèles régionaux sur l'alimentation du wapiti et son utilisation de l'habitat dans des aires de répartition estivale s'étendant sur 11 millions d'hectares dans l'ouest des états de l'Oregon et de Washington des États-Unis (région ci-après appelée Westside). Nous avons choisi la saison estivale parce que les contraintes nutritionnelles sur la condition et la reproduction du wapiti (p. ex. le pourcentage de réserves lipidiques) durant cette saison sont apparentes dans la plupart des régions de l'ouest des États-Unis. Notre hypothèse fondamentale était la suivante: l'utilisation de l'habitat par le wapiti durant l'été est régie par une série de covariables interdépendantes reliées au bilan énergétique, soit les gains (p. ex. ressources nutritionnelles, juxtaposition des sites pour s'alimenter et s'abriter) et les pertes (p. ex. proximité de chemins ouverts, topographie). Nous avons prédit que la femelle wapiti choisit toujours des sites plus nutritifs en été, ce qui donne un animal plus performant dans les paysages plus riches en nutriments. Nous avons aussi prédit que les facteurs de perturbations humaines, la végétation et la topographie auraient une influence sur la nourriture disponible durant l'été et sur l'utilisation des paysages par le wapiti, et prédit particulièrement que le wapiti éviterait les chemins ouverts et les sites d'alimentation loin de la frontière limitrophe entre la zone d'alimentation et la zone d'abri en raison de sa préférence pour des sites d'alimentation où il y a des endroits à proximité pour s'abriter de façon sécuritaire. Nos travaux avaient 2 objectifs principaux: 1) développer et évaluer un modèle sur l'alimentation qui permettrait d'estimer les conditions nutritionnelles régionales dans les aires de répartition estivale du wapiti à l'aide de prédicteurs qui tiendraient compte de l'écologie nutritionnelle du wapiti; et 2) développer un modèle sur l'utilisation de l'habitat en été qui intègre les projections issues du modèle sur l'alimentation avec d'autres covariables pour estimer la probabilité d'utilisation d'un habitat par le wapiti en tenant compte des processus écologiques qui déterminent l'utilisation d'un habitat. Pour atteindre nos objectifs, nous avons utilisé 25 ensembles de données déjà recueillis sur l'alimentation, la performance et la répartition du wapiti dans 12 sites d'étude. Nous avons démontré l'utilité de nos modèles régionaux à des fins de gestion en les appliquant dans 2 paysages de l'état de Washington.

Le modèle sur l'alimentation du wapiti a calculé l'énergie digestible des aliments du wapiti (EDA; kcal ED/g de fourrage ingéré) durant l'été. Les données d'entrée dans le modèle provenaient d'expériences sur la quête alimentaire effectuées avec des femelles wapitis en captivité et de mesures de terrain sur les caractéristiques des sites à petites échelles (~0,5 ha). Le modèle sur l'alimentation contenait une première série d'équations qui calculaient la quantité de biomasse fourragère en fonction des caractéristiques d'un site et une deuxième série qui calculaient l'EDA en fonction principalement de la biomasse fourragère. Nous nous sommes servis du modèle sur l'alimentation pour dresser une carte de l'EDA dans toute la région du Westside. Nous avons ensuite évalué la performance du modèle en comparant les projections faites par le modèle sur l'EDA au choix des ressources nutritionnelles faits par les wapitis et à des estimations faites sur le taux de gestation des femelles en lactation et sur leurs réserves lipidiques à l'automne, et ce, à l'échelle des populations. Pour modéliser l'utilisation de l'habitat du wapiti, nous avons compilé 13 ensembles de données télémétriques sur la femelle wapiti ($n = 173$) dans 7 sites d'étude (données recueillies entre 1991 et 2009 durant les mois de juin, juillet et août). Nous avons utilisé un modèle linéaire généralisé avec 5 des ensembles de données qui ont été combinés à des covariables écologiquement pertinentes sur l'alimentation, les perturbations humaines, la végétation et les conditions physiques afin d'estimer l'intensité d'utilisation de l'habitat à l'aide du modèle binomial négatif. Nous avons évalué la performance du modèle en cartographiant l'utilisation prévue de l'habitat à l'aide du modèle régional et en comparant les projections au nombre de sites utilisés par le wapiti à l'aide de 8 ensembles indépendants de données télémétriques.

Le modèle sur l'alimentation a expliqué un assez grand nombre de variations dans la biomasse fourragère ($r^2 = 0,46-0,72$) et contenait des covariables sur le couvert forestier de l'étage dominant, la proportion de feuillus dans le couvert forestier, la zone de végétation naturelle potentielle (VNP) et le site d'étude. Les équations sur l'énergie digestible des aliments (EDA) dans le modèle a expliqué environ 50% des variations de l'EDA ($r^2 = 0,39-0,57$) en fonction de la biomasse fourragère par zone de VNP et site d'étude. Une application à grande échelle du modèle sur l'alimentation dans la région du Westside a fait ressortir une quantité importante de paysages qui ne réussissaient pas à combler les besoins nutritionnels des femelles en lactation ($\leq 2,58$ kcal/g) et leurs faons, en particulier dans des forêts à couvert fermé à des altitudes modérées à la fois dans la chaîne côtière et dans le sud des monts Cascades. Les sites qui fournissaient une EDA égale aux ($> 2,58-2,75$ kcal/g) ou supérieure aux ($> 2,75$ kcal/g) besoins de base des femelles en lactation étaient peu courants ($< 15\%$ du site) ou rares ($< 5\%$ du site), respectivement, et se trouvaient principalement dans des forêts aux premiers stades de succession écologique, particulièrement à des altitudes plus élevées. Les wapitis sauvages évitaient les sites qui fournissaient une EDA sous les besoins de base et choisissaient des sites qui fournissaient une EDA $> 2,60$ kcal/g. Le pourcentage des aires de répartition des wapitis qui fournissaient une EDA à peu près égale ou supérieure à leurs besoins de base était fortement corrélé aux taux de gestation des femelles en lactation. Les réserves lipidiques des wapitis en

automne étaient fortement corrélées au pourcentage de leurs aires de répartition qui fournissaient une EDA supérieure à leurs besoins de base.

Le modèle régional sur l'utilisation de l'habitat par le wapiti qui corroborait le plus les données empiriques contenaient 4 covariables: EDA, distance au chemin ouvert le plus proche où circulent des véhicules motorisés, distance de la frontière limitrophe entre la zone d'alimentation et la zone d'abri et pente. Les wapitis ont préféré les habitats qui fournissaient une EDA relativement élevée et qui étaient loin des chemins, près de la frontière limitrophe entre la zone d'alimentation et la zone d'abri, et situés sur des pentes douces. Basés sur des coefficients normalisés, les changements dans la pente ($-0,949$) prédisaient le mieux l'utilisation de l'habitat, suivis de l'EDA ($0,656$), de la distance à la frontière limitrophe ($-0,305$) et de la distance à un chemin ouvert ($0,300$). Les ratios d'utilisation dans le modèle régional ont fait ressortir les changements suivants dans la probabilité relative que le wapiti utilise l'habitat: une augmentation de 111,2% dans l'utilisation de l'habitat par 0,1 unité d'augmentation de l'EDA, une augmentation de 22,7% dans l'utilisation de l'habitat par kilomètre additionnel entre le site d'alimentation et un chemin ouvert, une diminution de 8,1% dans l'utilisation de l'habitat par 100 m d'augmentation de la distance à la frontière limitrophe et une diminution de 5,3% dans l'utilisation de l'habitat par 1% d'augmentation dans la pente. Dans l'ensemble, le modèle régional a effectué une bonne validation, établissant une forte corrélation entre l'utilisation projetée et les valeurs observées pour les 4 sites de l'état de Washington ($r_s > 0,96$), mais une plus faible corrélation pour les sites situés dans le sud-ouest de l'état de l'Oregon ($r_s = 0,32-0,87$).

Nos résultats démontrent qu'il est possible d'utiliser des données sur l'alimentation recueillies à de petites échelles avec des wapitis en captivité pour prédire les ressources nutritionnelles à de grandes échelles et que ces projections sont directement reliées à la performance des wapitis en liberté et à leur utilisation de l'habitat dans l'ensemble de la région du Westside. Ces résultats montrent aussi l'importance d'inclure l'alimentation estivale dans l'évaluation de l'habitat et la planification du paysage pour le wapiti de la région du Westside. Les modèles peuvent être une source d'information pour établir les stratégies de gestion nécessaires pour atteindre les objectifs relativement aux wapitis qui se trouvent sur des terres boisées privées. Le modèle régional est un outil utile pour comprendre et documenter de façon spatialement explicite les besoins de l'habitat et la répartition des wapitis dans des paysages existants ou futurs. Les 2 exemples d'application sur le plan de la gestion ont démontré de quelle façon il était possible d'évaluer les effets de la gestion sur l'alimentation du wapiti et son utilisation de l'habitat à l'échelle des paysages et, par ricochet, les effets sur la performance et la répartition de l'animal. Les résultats illustrent également l'importance d'une gestion en fonction de l'alimentation combinée à d'autres covariables (c.-à-d. les chemins, la pente, la frontière limitrophe entre la zone d'alimentation et la zone d'abri) qui ont une influence sur l'utilisation des ressources nutritionnelles par le wapiti, et ce, afin d'obtenir la répartition désirée pour cet animal. Notre approche méta-analytique dans la modélisation de l'habitat fournit un cadre utile de recherche et de gestion des espèces fauniques qui intègre des besoins en habitat à une échelle grossière, en identifiant des éléments communs dans les profils d'utilisation de l'habitat qui sont robustes dans de multiples sites modélisés et dans une large aire géographique. L'utilisation de telles méthodes dans de futurs travaux de modélisation, notamment dans les programmes de surveillance et de gestion adaptative, continuera à faire avancer les connaissances en matière d'écologie et de gestion des espèces fauniques comme le wapiti.

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Modeling to Evaluate Elk Habitat: Contemporary Approaches for Western Oregon and Washington

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INTRODUCTION

Elk (*Cervus canadensis*) are among the most charismatic and popular wildlife species in North America. Their widespread distribution on public lands provides hunting and viewing opportunities that rival those for many species (Toweill and Thomas 2002). The economic contributions of elk hunting and viewing are substantial, with multi-million dollar benefits to rural towns throughout the western United States (Bunnell et al. 2002). The social contributions of elk to rural communities are equally strong, with elk hunting established as one of the most traditional activities associated with rural lifestyles (Bunnell et al. 2002). Native Americans throughout the central and western United States also considered elk an essential item in traditional tribal diets and integral to tribal culture and survival (McCabe 2002).

Despite the popularity of elk, the species also is one of the most controversial. The potential for elk and cattle to compete for food and space has been a topic of heated debate for over a century (Wisdom and Thomas 1996, Heydlauff et al. 2006). Herbivory by elk also has a strong but often ignored effect on vegetation development (Hobbs 1996, Wisdom et al. 2006, Averett et al. 2017). Poor nutrition and extensive road access on public lands can cause elk populations to shift distribution to adjacent private lands, diminishing public hunting and viewing opportunities (Wisdom and Cook 2000, Conner et al. 2001, Proffitt et al. 2010). In turn, when elk populations re-distribute seasonally or year-round to private lands, they can damage agricultural crops and commercial tree regeneration, and compete with domestic livestock for forage (Lyon and Christensen 2002, Heydlauff et al. 2006). Some private landowners design management specifically to entice elk populations to spend more time on private lands for lease hunting, thereby reducing opportunities for viewing and hunting on public lands (Toweill and Thomas 2002).

Issues of elk distribution are intimately linked with how landscapes are managed among land ownerships and management jurisdictions (Wisdom and Cook 2000, Lyon and Christensen 2002, Cleveland et al. 2012, Proffitt et al. 2013). To address these issues, accurate prediction of how elk use and

respond to changes in habitat conditions within and across these large landscapes is essential. We addressed this need with the development of regional nutrition and habitat-use models for application on summer ranges in western Oregon and Washington (hereafter, Westside region), an area of 11.8 million ha between the crest of the Cascade Range and the Pacific Ocean in these 2 states (Fig. 1).

Our work was motivated by recommendations of the Sporting Conservation Council (SCC), a federal advisory committee that advised the Secretaries of Agriculture and Interior of the United States Government in the 2000s under the Federal Advisory Committee Act of 1972 (Public Law 92-46, 6 Oct 1972). In a letter sent to the Secretaries on 4 December 2007, the SCC formally endorsed development of new elk habitat models for the Westside region to address urgent land management needs of federal agencies (Sporting Conservation Council 2007). The SCC addressed 2 key management needs in their dialogue with federal managers: 1) new models to accurately predict elk distributions within and across land ownerships in response to forest management and human disturbances at landscape scales; and 2) new models that reflect contemporary scientific paradigms and methods.

Deficiencies in past habitat modeling approaches for elk motivated the rationale and direction of the SCC. Elk habitat models first developed in the late 1970s and 1980s (Brunt and Ray 1986; Thomas et al. 1979, 1988; Leege 1984; Lyon et al. 1985; Wisdom et al. 1986) provided practical methods to evaluate and manage habitat at landscape scales based on key variables that affect or account for elk use of landscapes. The models, however, were based on small-scale, observational studies with little or no spatial replication; did not accurately quantify the effects of multiple, interacting covariates; were not spatially explicit or were difficult to incorporate spatially; typically ignored elk nutrition; and often failed to clearly quantify the response variable, instead relying on a qualitative rating of habitats difficult to interpret. Most importantly, model predictions were not validated with independent data.

One of the 1980s models was developed to evaluate elk distributions and landscapes in the Westside region (referred to as the 1986 model; Wisdom et al. 1986). The 1986 model had 4 covariates: forage quality, open road density, cover quality, and size and spacing of cover and forage areas. The model was

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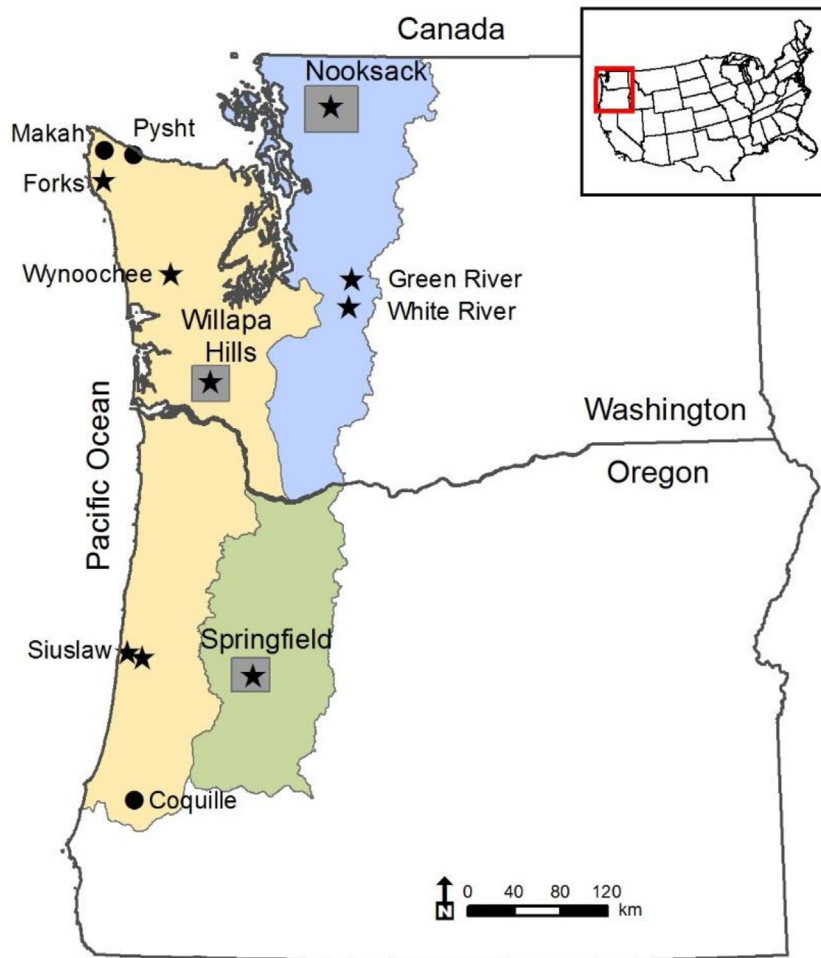


Figure 1. Location and distribution of 12 study areas in western Oregon and western Washington, USA (Westside region) where data were collected (1988–2009) to develop or validate elk nutrition and habitat-use models. Three study areas used to develop independent prediction equations for dietary digestible energy (DDE) and forage biomass using captive elk are denoted by shaded squares; color shading indicates the respective regions to which those equations apply: Nooksack, Willapa Hills, and Springfield. Study areas used for comparisons of predicted DDE levels with pregnancy rates and autumn body fat of wild elk are denoted by stars. Study areas used only for habitat use modeling are denoted by circles.

intended for use within and across land ownerships at watershed or larger landscape scales, similar to our current modeling (Rowland et al. 2018). Despite these similarities, the 1986 model had deficiencies like those of other elk habitat models of the 1970s and 1980s. Most importantly, the 1986 model was never validated with independent data, an essential requirement identified for its use (Wisdom et al. 1986).

Here we describe hypotheses, objectives, rationale, and a conceptual framework for our approach to nutrition and habitat-use modeling in the Westside region. We first describe the Westside region, status of elk populations, and current management issues as context to introduce our modeling approaches; we then provide details of modeling methods, results, and interpretations (Cook et al. 2018, Rowland et al. 2018, Wisdom et al. 2018b).

WESTSIDE MODELING REGION AND ELK

The Westside region is bounded to the East by the crest of the Cascade Range, to the West by the Pacific Ocean, to the North by the Canadian border, and to the South by the Coquille and Umpqua Rivers in southwest Oregon (Fig. 1). The region is

dominated by coniferous, temperate rainforests and is considered one of the most productive ecosystems on earth (Franklin and Dyrness 1988). The region's environment has similar climate, geology, and vegetation types but follows a north–south gradient of higher to lower precipitation and associated changes in productivity (Appendix A, available online in Supporting Information; Franklin and Dyrness 1988). High amounts of precipitation (>200 cm annually) occur primarily during fall–spring in coastal and high-elevation forests (Franklin and Dyrness 1988). Vast forests of Douglas-fir (*Pseudotsuga menziesii*), western hemlock (*Tsuga heterophylla*), and western redcedar (*Thuja plicata*) dominate landscapes at lower and mid-elevations, and forests of Pacific silver fir (*Abies amabilis*) and mountain hemlock (*T. mertensiana*) dominate at higher elevations. Alpine communities are prevalent in the high montane areas of the Cascade Range and Olympic Mountains.

Forested lands are common above valley floors, and agricultural lands and urban areas dominate valley bottoms. Over 7 million people occupy urban areas, but rural areas are sparsely populated. Land ownerships include national forests or other federal lands (36%), private forests (44%), state lands (8%), agricultural areas

(8%), and urban areas or other lands (4%). Forested lands provide a variety of goods and services with emphasis on timber production in private forests (Adams and Latta 2007).

Elk populations in the region vary in size and distribution by geographic area and management regimes on different land ownerships (Washington Department of Fish and Wildlife 2002*a, b, c*, 2004, 2008, 2013; Oregon Department of Fish and Wildlife 2003; McCorquodale et al. 2012). Current populations are a mix of Roosevelt (*C. c. roosevelti*) and Rocky Mountain elk (*C. c. nelsoni*) subspecies, resulting from multiple translocations of Rocky Mountain elk into the native range of Roosevelt elk that encompasses the Westside region (Toweill and Thomas 2002; Washington Department of Fish and Wildlife 2002*a, b, c*, 2004, 2008, 2013). Populations are mostly stable but substantially lower in some state management units compared to the latter half of the 20th century, whereas a few are increasing (Appendix A; Washington Department of Fish and Wildlife 2002*a, b, c*, 2004, 2008, 2013; Oregon Department of Fish and Wildlife 2003). The only other wild ungulate that is common to the Westside region is black-tailed deer (*Odocoileus hemionus columbianus*), which largely co-occur with elk (Witmer et al. 1985). Common predators of elk in the Westside region include black bears (*Ursus americanus*), cougars (*Puma concolor*), coyotes (*Canis latrans*), and bobcats (*Lynx rufus*). Gray wolves (*Canis lupus*) have been functionally extirpated from the region for many decades, including the time periods of data collection used in our modeling.

Although elk remain widely distributed in the region, early-seral vegetation has declined substantially during the past 25 years (Spies et al. 2007, Swanson et al. 2011). Because of mild temperatures and high precipitation, forest succession is rapid in the Westside region, and early-seral vegetation is quickly replaced by dense overstory canopies 10–20 years after timber harvest or stand-replacement fires (Hall et al. 1985). Up to 35% of forested landscapes in the Westside region burned at 25-year intervals or longer since at least the 1400s, helping to maintain a mosaic of early-seral vegetation communities (Weisburg and Swanson 2003). The size and frequency of disturbances required to establish these communities has declined sevenfold in the past 25–50 years (Weisburg and Swanson 2003).

Recent declines in early-seral vegetation have been concentrated on federal lands in response to a major reduction in timber harvest (Thomas et al. 2005, Adams and Latta 2007) in the early 1990s, based on direction established in the Northwest Forest Plan (U.S. Department of Agriculture [USDA] Forest Service and U.S. Department of the Interior [USDI] Bureau of Land Management 1994*a, b*). Timber harvest on many private lands increased over the same period (Adams and Latta 2007), resulting in a greater percentage of private land area in early-seral vegetation (Cook et al. 2018). However, the duration of early-seral vegetation has been truncated substantially by intensive conifer regeneration practices (Swanson et al. 2011, 2014).

Because early-seral forest vegetation provides highly nutritious forage for elk in the region (Witmer et al. 1985, Jenkins and Starkey 1996, Cook et al. 2016), the uneven distribution of early-seral vegetation on public versus private lands has raised concerns about maintaining elk numbers on public lands for hunting and

viewing (USDA Forest Service 2001*a, b*; Washington Department of Fish and Wildlife 2002*a*). The widespread loss of early-seral vegetation is considered central to the current nutritional challenges for elk in the Westside region, and the absence of early-seral vegetation on public forests has resulted in nutritionally depauperate conditions (Cook et al. 2013, 2016). Thus the main management issue for Westside elk is not population size *per se*, but the disproportionately low numbers of elk on public forest lands (USDA Forest Service 2001*a, b*; Washington Department of Fish and Wildlife 2002*a*).

In addition, roads open to motorized traffic and trail-based summer recreational uses are common on public lands in the Westside region, and private lands often are closed to public access. On summer range, shifts in elk distribution away from open roads (Rowland et al. 2000, 2005; Wisdom et al. 2005*b*; Frair et al. 2008; Montgomery et al. 2012), and trail-based recreational uses are common on public forests (Wisdom et al. 2005*a*). Consequently, the potential for elk in the Westside region to shift distributions to private lands, in response to reduced nutrition and increased road and trail access on public lands, served as context for our modeling.

Study Areas and Data Sets for Regional Inference

Boundaries of the Westside region encompassed 12 study areas that we used for modeling elk nutrition and habitat use (Fig. 1; Table 1). Study areas included geographic and environmental variation in vegetation types, elevational and climatic gradients, forest structural conditions, and land ownerships (Fig. 1; Appendix A; Hall et al. 1985; Franklin and Dyrness 1988; Cook et al. 2016, 2018; Rowland et al. 2018). Consequently, the region's boundaries represent a logical, targeted inference space for modeling and applications.

We used 25 data sets from the 12 study areas for analyses (Fig. 1; Table 1). We defined a data set as a specific type of empirical data (nutrition, animal performance, or habitat use) collected within a given study area and time period that we used to develop or validate nutrition or habitat-use models (Table 1; Appendix A). We defined a study area as a distinct geographic area within which ≥ 1 data sets were collected. We defined validation as the evaluation of model predictions with independent observations of those predictions, or evaluation of hypothesized relationships of model predictions with animal performance or habitat use. Model validation therefore is any independent evaluation of *a priori* expectations of model performance, an inclusive approach that follows definitions and guidance of Power (1993), Rykiel (1996), and Johnson (2002).

Of the 25 data sets used for modeling, 3 were composed of nutrition data (e.g., estimates of elk nutritional resources during summer) collected from grazing trials of captive elk that served as the foundation for development of nutrition models (Table 1; Cook et al. 2016, 2018). Nine additional data sets were composed of estimates of animal performance (pregnancy rates and body fat estimates from lactating female elk; Cook et al. 2013) used for validation of nutrition models (Cook et al. 2018). Thirteen other data sets were composed of animal telemetry locations used to develop or validate habitat-use models (Table 1).

Table 1. Study areas, data sets and years of data collection, type of data collected, and use of data sets in elk nutrition and habitat-use modeling in western Oregon and Washington, USA.

Study area	Data set ^a	Data type	Modeling use
Coquille	Coquille North 1991–1992	Habitat use	Habitat-use model validation
	Coquille North 1993–1994	Habitat use	Habitat-use model validation
	Coquille South 1991–1992	Habitat use	Habitat-use model validation
	Coquille South 1993–1994	Habitat use	Habitat-use model validation
Forks	Forks 2000–2003	Animal performance	Nutrition model validation
	Quileute 2006–2008	Habitat use	Habitat-use model validation
Green River	Green River 1998–2006	Animal performance	Nutrition model validation
	Green-Cedar 2008	Habitat use	Habitat-use model development
	Green-Cedar 2006–2007, 2009	Habitat use	Habitat-use model validation
Makah	Makah 2000–2003	Habitat use	Habitat-use model validation
Nooksack	Nooksack 2002	Nutrition	Nutrition model development
	Nooksack 2000–2002	Animal performance	Nutrition model validation
	Nooksack 2008–2009	Habitat use	Habitat-use model validation
Pysht	Pysht 2009	Habitat use	Habitat-use model development
Siuslaw 1	Siuslaw 1 1988–1989	Animal performance	Nutrition model validation
Siuslaw 2	Siuslaw 2 1988–1989	Animal performance	Nutrition model validation
Springfield	Springfield 2000	Nutrition	Nutrition model development
	Springfield 2000–2002	Animal performance	Nutrition model validation
	Springfield 2000–2002	Animal performance	Nutrition model validation
White River	White River 1998–2007	Habitat use	Habitat-use model development
	White River 2004	Habitat use	Habitat-use model development
	White River 2005	Habitat use	Habitat-use model development
	White River 2007	Habitat use	Habitat-use model development
Willapa Hills	Willapa Hills 2001	Nutrition	Nutrition model development
	Willapa Hills 2000–2002	Animal performance	Nutrition model validation
Wynoochee	Wynoochee 2003–2005	Animal performance	Nutrition model validation

^a Data sets for habitat-use modeling were assigned to modeling or validation areas by Rowland et al. (2018).

CONTEMPORARY HABITAT MODELING FOR THE WESTSIDE REGION

Hypotheses, Objectives, and Rationale

Recent advances in data collection technologies and analytical methods for habitat modeling provided a significant opportunity to address the deficiencies associated with the 1986 model. During the mid-2000s, new data on elk nutrition, habitat use, and animal performance were collected across a variety of study sites in the region (Fig. 1; Table 1; Appendices A, B, available online in Supporting Information; Cook et al. 2013, 2018; Rowland et al. 2018). These data were not collected under any overarching design or unifying theme, but their availability across multiple study areas and conditions provided an opportunity to initiate a meaningful new round of model development and validation (Table 1). For our modeling, we define habitat as the resources and conditions present in an area that produce occupancy, including survival and reproduction needed for persistence of an organism (adapted from Hall et al. [1997]). This definition relates habitat to the environmental requirements of a species, not just vegetation.

Our goal was to replace the 1986 model using these new data in contemporary landscape models of nutrition and habitat use that could accurately account for elk distributions during summer across the Westside region. We focused on summer (Jun–Aug) because nutritional resources in most forest successional stages in the Westside region do not meet the maintenance requirements of lactating female elk during this period (Cook et al. 2016). Consequently, conditions on many summer ranges pose substantial constraints on animal condition, pregnancy rates, and lactation status in the region (Cook et al. 2013).

The overarching hypothesis driving our work was that elk habitat use during summer is driven by a collection of interacting covariates that influence energy balance: acquisition (e.g., nutritional resources), and expenditure (e.g., travel on steep slopes). We predicted that female elk consistently select areas of higher summer nutrition, resulting in better animal performance in more nutritionally rich landscapes. We also predicted that non-nutritional factors of human disturbance, vegetation, and topography further affect summer elk use of landscapes and available nutrition. Because the ecological mechanisms that drive these hypotheses operate across space and time, we further predicted that the same or similar nutrition and habitat-use models would perform well across the environmental conditions of the Westside region and years of data collection.

We had 2 major objectives to support our goal: 1) to develop and evaluate a nutrition model that could accurately estimate region-wide nutritional conditions for elk on summer ranges, based on predictors that reflect the ecological processes of animal nutrition; and 2) to develop and validate a summer habitat-use model that integrates the nutrition model predictions with other covariates to estimate relative probability of use by elk. For the second objective, we used a combination of covariates that most accurately predict and account for ecological processes of elk habitat use in the region (Fig. 2). Our objectives relied on analyses conducted at the population scale (Cook et al. 2018, Rowland et al. 2018), which combined attributes of second- and third-order selection defined by Johnson (1980). This combined order of selection provided population-level estimates of nutrition and habitat use across the range of the species in the Westside region (Wisdom et al. 2018b).

We identified 2 requirements to meet objectives. First, the models should be designed to gain new knowledge of the ecological

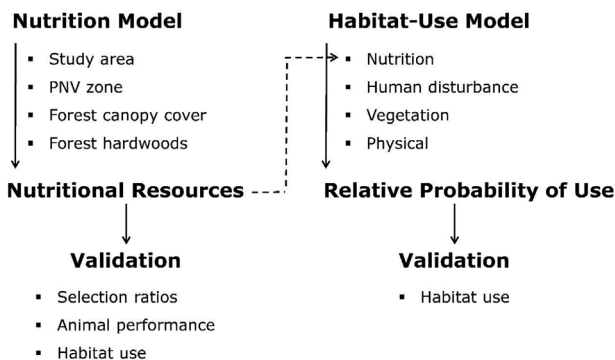


Figure 2. Conceptual structure of elk nutrition and habitat use models developed and validated for the Westside region, western Oregon and western Washington, USA. Types of covariates considered during model development and types of data used for validation of each model are shown below each model or type of validation. Three zones of potential natural vegetation (PNV) occurred in the Westside region: western hemlock at lower elevations, Pacific silver fir at moderate elevations, and mountain hemlock at higher elevations.

processes that serve as drivers of elk nutrition and habitat use. The literature on habitat use contains many models that provide useful predictions but not always with understanding of how model covariates represent underlying ecological processes that drive animal use in a robust manner across time and space (Morrison 2001, 2012). Second, these types of process-driven covariates, referred to as mechanistic covariates, should be foundational to modeling to ensure robust management applications. We define a mechanistic covariate as one that explicitly represents a species' habitat requirements and that can be manipulated by managers in a cause-effect manner to change nutrition or habitat use. Mechanistic covariates should have a documented or highly plausible connection to the ecological processes of energy acquisition or energy loss that underlie the species' ecology, nutrition, and habitat choices (Rowland et al. 2018).

Modeling Structure and Approach

We established a modeling structure (Fig. 2) to address our hypotheses, predictions, and objectives with use of the 25 data sets. The structure follows the philosophy and guidance of Levins (1966), who emphasized process-driven models sufficient to meet objectives with minimal parameters. This approach follows the principle of parsimony, where the balance between models with strongest empirical support and lowest number of parameters is identified (Burnham and Anderson 2002).

The nutrition model was designed as a stand-alone tool to estimate and map nutritional resources based on elk diet quality. These resources varied empirically by potential vegetation type, structural condition, and topography on Westside summer ranges (Cook et al. 2016, 2018). We assumed that fine-scale nutrition data collected from captive elk in the Westside region (Cook et al. 2016), rescaled to regional nutrition models, would reflect the nutritional levels and landscape-selection patterns of wild elk, and would correlate well with population performance metrics of pregnancy rates and body fat. Predictions from the nutrition model are intended for spatial application at scales of the local or regional landscape, or can be obtained using the model in a tabular format for planning scenarios (Rowland et al. 2013, Cook et al. 2018, Wisdom et al. 2018b).

The habitat-use model estimates the relative probability of animal use (Nielson and Sawyer 2013) on the same summer ranges and landscape scales in which nutrition is estimated (Rowland et al. 2018). We used elk telemetry locations to model the intensity of use in relation to habitat characteristics (Nielson and Sawyer 2013), which is considered an analysis of habitat use. Note that this definition is somewhat different than an analysis of habitat selection (Manly et al. 2002). By modeling habitat use along a continuum, more information is gained about the relationships between habitat characteristics and probability of use by the animal (Rowland et al. 2018). We modeled habitat use by considering covariates in 4 categories: nutrition (the response variables from the nutrition model), human disturbance, vegetation, and physical conditions that best explain use by elk (Fig. 2; Rowland et al. 2018).

Neither model predicts carrying capacity (Hett et al. 1978, Hobbs et al. 1982, Hobbs and Swift 1985, Beck et al. 2006), but both are necessary components of carrying-capacity models. Nutrition is the foundation for estimation of carrying capacity (Caughley 1979, Hobbs et al. 1982), and factors of human disturbance can reduce carrying capacity (Beck et al. 2006). In addition, neither the nutrition nor the habitat-use model was designed to predict population characteristics like density, recruitment, survival, or growth rate because these characteristics can be greatly influenced by additional factors such as predation and hunting (Sinclair and Krebs 2002, Johnson et al. 2013, Clark 2014). The habitat-use model was designed to predict elk distribution (relative probability of elk use) within local and regional landscapes, however, and these predictions represent the relative abundance of elk at those scales (Rowland et al. 2018).

Both models evaluate summer conditions for elk populations assumed to be hunted later in the year, either on the same summer ranges or on different fall ranges. Populations that live year-round near or within urban areas where hunting is prohibited behave differently than wild, hunted elk herds (Thompson and Henderson 1998, Starr 2013). Our objectives did not include modeling habitat use by unhunted elk in these special situations.

Our modeling approach used different types of validation (see definition provided earlier). For nutrition modeling, we did not evaluate predicted versus observed nutrition because independent data were not available to do so (i.e., we did not have direct observations of elk diet quality from captive elk in additional study areas that could be withheld for validation). Instead, we evaluated model performance based on *a priori* hypotheses of how nutrition model predictions related to selection ratios, measures of population performance, and habitat use (Cook et al. 2018, Rowland et al. 2018). These more-inclusive types of evaluation and validation have been advocated and used in ecological modeling per Rykiel (1996). For habitat-use modeling, predictions were validated in the more traditional sense, using independent observations of habitat use from data sets and study areas withheld from model development (Rowland et al. 2018). Cook et al. (2018) and Rowland et al. (2018) provide detailed rationale, methods, results, and interpretations of our modeling structure and approach for nutrition and habitat use, respectively. Wisdom et al. (2018b) then describe key implications for research and modeling of wildlife, provide example applications for elk, and discuss management challenges.

Development and Evaluation of a Landscape Nutrition Model for Elk in Western Oregon and Washington

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INTRODUCTION

Nutrition influences productivity of ungulates by affecting many aspects of animal performance, including nutritional condition (defined as the state of body components [principally fat and lean mass] controlled by nutrition, which influences an animal's future fitness [Harder and Kirkpatrick 1994]), ovulation, timing of breeding and subsequent parturition, juvenile growth, primiparity, and susceptibility to a variety of causes of mortality (Verme and Ullrey 1984; Cook et al. 2004, 2013). Although nutritional limitations of ungulates in winter are commonly recognized (Wallmo et al. 1977, Houston 1982, Coughenour and Singer 1996), world-wide documentation of limiting effects of nutrition in summer and early autumn is increasing (Hjeljord and Histol 1999, Dale et al. 2008, Cook et al. 2013, Hurley et al. 2014, Rolandsen et al. 2017). Such also is the case in the temperate rainforests in western Oregon and Washington (hereafter, the Westside region), where depressed pregnancy rates and low autumn body fat levels of elk are well-documented (Trainer 1971, Smith 1980, Harper 1987, Stussy 1993, Cook et al. 2013). Nevertheless, substantial variation in nutritional condition and pregnancy rates of elk populations exists across the region (Cook et al. 2013), at least in part as a function of vegetation disturbance, succession, and ecological context (Merrill 1987, 1994; Hutchins 2006; Cook et al. 2016).

Because nutrition has quantifiable, cause-and-effect influences on nutritional condition, reproduction, and survival in ungulates, nutritional ecology offers a quantitative basis for scaling-up key relations between individual animals and their habitats to populations (Fryxell 1991, Parker et al. 1999). It also offers value for landscape assessments and resource planning on behalf of large ungulates. Many approaches have been used to quantify nutritional resources for ungulates, including 1) surveys of forage quantity and, sometimes, forage quality for carrying capacity models (Hanley et al. 2012); 2) complex, spatially explicit simulation models intended to predict distribution and

performance of ungulates (e.g., Coughenour and Singer 1996, Moen et al. 1997); and 3) a variety of proxy variables assumed to represent nutritional influences (e.g., Thomas et al. 1988, Johnson et al. 2001, Garrouette et al. 2016). Whatever modeling approach is used, considerable uncertainty exists regarding the relevance and rigor of measures used to represent nutritional resources (Babin et al. 2011). For example, proxy variables and even some standard metrics of forage quality and quantity have rarely been validated as measures of nutritional resources (Searle et al. 2007, Cook et al. 2016). Also, appropriate approaches remain unclear for translating nutritional responses of herbivores to vegetation at fine scales to estimate individual animal performance and population dynamics at broad scales, especially in spatially and temporally heterogeneous environments (Owen-Smith 2002, Hobbs 2003). Particularly for management and planning applications, nutrition models should reflect influences of disturbance, succession, and ecological context and integrate these with routine land management and landscape planning protocols (Haufler 1994).

We used foraging ecology data collected using captive elk in western Oregon and Washington, USA (Cook et al. 2016) to develop a nutrition model designed for landscapes in summer and early autumn that can be linked with a spatially explicit habitat-use model (Rowland et al. 2018) for practical management applications (Wisdom et al. 2018b). In the temperate rainforests of western Oregon and Washington, nutritional value of plant communities, as indexed by digestible energy (DE) content of forage consumed by elk, is strongly driven by forest succession, disturbance, and ecological site conditions (plant phenology, climate, soils, composition and abundance of plant species; Merrill 1994, Merrill et al. 1995, Cook et al. 2016). Thus, we strove to develop our nutrition model to reflect these influences in landscapes ranging from relatively dry, low-elevation forests to wet and cold forests near timberline. Incorporating successional influences also should facilitate predictions of changes in nutritional resources over time and identify management options for modifying the nutritional environment across landscapes (Haufler 1994). Cook et al. (2016) developed regression equations to predict dietary digestible energy (DDE)—the content of digestible energy (kcal/g) in elk diets—as a function of the types of forage available to foraging elk, and used these

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equations to describe successional trajectories of DDE from newly harvested stands to late seral stages for each of the major vegetation zones of the region. However, they did not provide equations to estimate biomass of the forage classes that are required as input data to predict DDE. We adopted these DDE equations in our nutrition model, developed equations to predict these forage-class amounts based on environmental data (e.g., overstory canopy cover, ecological site potential) that were readily available in geographic information systems (GIS), and combined them into an overall nutrition model. Although Cook et al. (2016) explored various currencies for their prediction equations (e.g., energy, protein, intake rates of energy and protein), they concluded that DDE was the most valuable for describing nutritional value of plant communities and identifying nutritional limitations; it also was the most predictable nutritional metric for elk in the Westside.

Past work has established that elk performance, as measured by indices of nutritional condition and pregnancy rates, is relatively low in many elk populations (Trainer 1971, Harper 1987, Cook et al. 2013), and that nutritional value of many vegetation types provide inadequate nutrition for lactating elk and their calves during summer (Cook et al. 2016). However, direct links between fine-scale measures of nutritional value of vegetation types and broad-scale measures of performance (population-level pregnancy rates and nutritional condition) largely remain untested. Elk may compensate for poor nutritional resources by strongly selecting for those vegetation types that offer adequate nutrition and avoiding those that do not (Moen et al. 1997). In addition, other environmental influences such as herbivore density or harassment by predators or humans may be responsible for relatively poor performance in some populations. Hence, our overarching hypothesis was that elk preferentially seek those vegetation types that provide relatively high nutrition to compensate for inadequate nutritional resources, but compensation may be incomplete and elk performance reduced on elk ranges with strongly depauperate nutritional resources. We had the following predictions: 1) vast areas of our study region are dominated by nutritional resources that are inadequate (<~2.6 kcal/g of DDE/g) to support high pregnancy rates and relatively high body fat levels; accordingly, elk will significantly select for areas that provide relatively high levels of DDE (e.g., >~2.6 kcal/g where low DDE levels predominate); 2) population-level pregnancy rates and autumn body fat levels of lactating elk will vary with estimated DDE expressed as percentages of elk ranges offering differing levels of DDE; and 3) relatively high levels of body fat (i.e., ≥12%) are more likely to occur on elk ranges that offer a higher proportion of good nutrition (≥2.75 kcal/g) than ranges that do not but nevertheless are able to support high pregnancy rates (Cook et al. 2004). Our references to differing levels of DDE and their relevance to elk reflect findings of Cook et al. (2004) (Table 2).

We had 5 primary objectives for the nutrition model: 1) to use the model to construct spatially explicit nutritional resource maps that predict DDE across ecological gradients and forest succession using a GIS; 2) to assess the nutrition model developed with fine-scale data of vegetation characteristics by evaluating relationships between predicted DDE and nutritional resource use by elk, autumn body fat levels, and pregnancy rates

Table 2. Classes of dietary digestible energy (DDE) used to summarize nutrition modeling results for elk (modified from Cook et al. 2004). Basic requirements of lactating female elk during summer are met at the high-marginal class.

Class	Description	DDE (kcal/g)
1	Poor	<2.40
2	Low-marginal	2.40–2.58
3	High-marginal	>2.58–2.75
4	Low-good	>2.75–2.83
5	High-good	>2.83–2.90
6	Excellent	>2.90

for elk populations at broad scales; 3) to explicitly test our predictions that elk would select for areas offering relatively high DDE and that pregnancy rates and autumn body fat levels would vary with predicted levels of DDE across landscapes; 4) to summarize current nutritional resources for Westside elk and thus illustrate differences among ecological provinces and landowners; and 5) to integrate the nutritional resources map with other environmental variables to develop a habitat-use model for the study region (Rowland et al. 2018).

STUDY AREAS

We acquired data to develop our nutrition model from 3 study areas located in the temperate rainforests of western Oregon and Washington, USA (Fig. 1; Table 1; see Cook et al. 2016 for additional details). The Nooksack area was located in the Cascade foothills and mountains south of Mt. Baker, Washington, the Willapa Hills area was located in the Coast Range of southwest Washington, and the Springfield study area was in the foothills of the central Oregon Cascades (Appendix A). At Nooksack, topography was relatively steep, with broad, glaciated valley bottoms and elevations ranging from 100 m to 1,400 m. Topography was gently rolling to steep at Willapa Hills and Springfield and elevation ranged from 100 m to 700 m, with occasional mountain peaks to 1,000 m. Annual precipitation varied from 100 cm to 300 cm, depending on elevation and latitude (Daly et al. 1994).

Three primary forest zones, based on potential natural vegetation (PNV) categories (Franklin and Dyrness 1988, Henderson et al. 1992), predominated across the 3 study areas: the western hemlock zone (WHZ) at lower elevations, the Pacific silver fir zone (SFZ) at moderate elevations, and the mountain hemlock zone (MHZ) at higher elevations. Alpine areas were present at Nooksack, but we did not acquire data from this type. The higher elevation forest zones—SFZ and particularly the MHZ—were well represented only in the Nooksack study area. In general, diversity of understory vegetation increased with elevation across the WHZ, SFZ, and MHZ and declined as plant succession advanced (Franklin and Dyrness 1988, Cook et al. 2016).

For evaluating the nutrition model, we used data on pregnancy rate and autumn body fat from lactating female elk in 7 wild populations described by Cook et al. (2013) and 2 populations described by Stussy (1993) (Fig. 1; Table 3). These included the Forks, Wynoochee, and Willapa Hills populations in the Coast Range of western Washington; the Nooksack, Green River, and the White River populations in the Cascades of western Washington; a population near Springfield in the Cascades of western Oregon; and 2 adjacent populations (Stussy 1993) in the

Coast Range of west-central Oregon. Data from elk in the Mount St. Helens population in southwest Washington were presented by Cook et al. (2013) but not used herein for statistical analyses for 2 reasons. First, the autumn fat data were collected during an October drive-trapping operation within a very small sub-portion of the population's range that was still highly affected by the eruption of Mount St. Helens (Cook et al. 2013). Second, the pregnancy data were collected during spring and thus could not be partitioned by lactation status as they were for the other populations (i.e., females with a calf at heel commonly cease lactating before spring).

In general, elk in the Coast Range largely occurred within the WHZ, and those in the Cascade Range were in the WHZ at low to moderate elevations and in the SFZ and MHZ at higher elevations. However, elk at Springfield had little access to the higher elevation PNV zones. Elk were considered to be the Roosevelt subspecies for all populations in the Coast Range and the Rocky Mountain subspecies in the Cascades (Cook et al. 2013). Elk were predominately non-migratory, although some elk populations of the Washington Cascades migrated to higher elevation ranges. Study area descriptions were presented by Cook et al. (2013) and Stussy (1993), and Appendix A contains additional descriptions of the Nooksack, Green River, White River, and Forks areas.

METHODS

Background

Cook et al. (2016) used 25 captive adult, lactating Rocky Mountain elk and their calves to investigate foraging dynamics in the 3 study areas of Nooksack, Willapa Hills, and Springfield. In addition, they measured overstory and understory vegetation characteristics in ~1-ha macroplots at these 3 study areas, with 1 field season (late Jun–Oct 2000–2002) devoted to each. Foraging behavior was sampled in macroplot pens (electrified enclosures),

with 4 elk and their calves per pen and 3–4 pens operated simultaneously. Bite-count methods (Collins and Urness 1983, Wickstrom et al. 1984, Parker et al. 1999) were used to estimate key dietary metrics for elk, including patterns of selection among forage species, and intake rates of dry matter, DDE, and dietary digestible protein content, with intake rates of these nutrients expressed per minute and per 24-hour period. Digestible energy and protein were determined using detergent fiber assays coupled with assays of tannin astringency (Robbins et al. 1987a, b). Overstory and understory vegetation sampling was conducted along 5 parallel transects. Understory vegetation included current year's dry-matter biomass of each vascular plant species clipped in 2, 2-m² circular plots per transect ($n = 10$ clip plots/macropoint). Measures of overstory characteristics included canopy cover (CC) determined using a moosehorn ocular sighting tube (Bunnell and Vales 1990, Cook et al. 1995), stand height, mean diameter at breast height, and basal area using a variety of standard forest mensuration techniques, and composition of tree species along the transects. Evidence of thinning and PNV type (Franklin and Dyrness 1988, Henderson et al. 1992) was recorded, and stand age was acquired from landowner records. At each study area, Cook et al. (2016) sampled approximately 30 macroplots using the captive elk and an additional ~90 macroplots where only vegetation characteristics were measured.

The equations developed by Cook et al. (2016) to predict DDE were generally a function of the biomass (kg/ha) of palatable and relatively nutritious food in the plant community. They partitioned plant biomass into 3 selection categories: those that elk significantly selected (selected biomass; SB), those significantly avoided (avoided biomass), and those consumed in proportion to availability (neutral biomass; NB). Avoided biomass, mainly shade-tolerant evergreen shrubs, conifers, and evergreen ferns, composed 80% to 95% of the understory vegetation biomass in mid- and late-seral stages, particularly in

Table 3. Characteristics of elk populations in western Oregon and Washington, USA, used for elk nutrition model evaluation. Data are from prime-age (2–14 yr), lactating elk only unless otherwise noted. Body fat and pregnancy data were from Cook et al. (2013) and Stussy (1993), the latter for the 2 Siuslaw populations.

Population	Years sampled	n^a	Autumn body fat (%) ^b	Pregnancy (%) ^c	Study area method ^d	Number of elk locations	Study area size (ha)
Forks, WA ^e	2000–2003	31	6.0	61	MCP + 500	400	27,847
Green River, WA	1998–2006	58	10.0	91	Study area		39,072
Nooksack, WA	2000–2002	21	12.5	95	MCP + 500	556	49,061
Springfield, OR	2000–2002	23	10.2	73 ^f	MCP + 500	444	14,699
Siuslaw 1, OR	1988–1989	13	3.2	21	Study area		17,743
Siuslaw 2, OR	1988–1989	13	3.7	46	Study area		25,096
White River, WA	1998–2007	72	11.0	95	Study area		58,060
Willapa Hills, WA	2000–2002	22	6.2	78	MCP + 500	621	18,759
Wynoochee, WA	2003–2005	40	6.0	67	MCP + 500	1,719	76,444

^aNumber of unique elk captured at each study area (most elk were captured and sampled at least twice/yr for 2 yr). Relocations from these elk also were used to calculate home range boundaries except for the Siuslaw, Green, and White River study areas.

^bEstimated from scaled LIVINDEX using ultrasonography of rump fat and a body condition score (Cook et al. 2001, 2010). For elk in the Siuslaw populations, body fat was estimated using the trimmed kidney fat index (Riney 1955) and converted to estimates of percent body fat using equations presented in Cook et al. (2001) for elk ranging from 4–12 years old (considered prime age in this study).

^cDetermined via ultrasound and palpation with the negatives confirmed with Pregnancy-Specific Protein B (Noyes et al. 1997). For the Siuslaw populations, pregnancy was determined by examination of uteri from uncollared hunter-harvested elk (Stussy 1993).

^dMCP + 500 = minimum convex polygon around elk relocations plus 500-m buffer. Study area boundaries for the Siuslaw populations were provided by R. Stussy (Oregon Department of Fish and Wildlife, personal communication; Stussy 1993) and by D. Vales (Muckleshoot Indian Tribe, personal communication) for the White and Green River populations.

^ePopulation overlaps with the Quileute telemetry data set.

^fPregnancy rates are from spring captures based on those females known to be lactating the previous autumn ($n = 15$) because the autumn captures were too early to detect pregnancy.

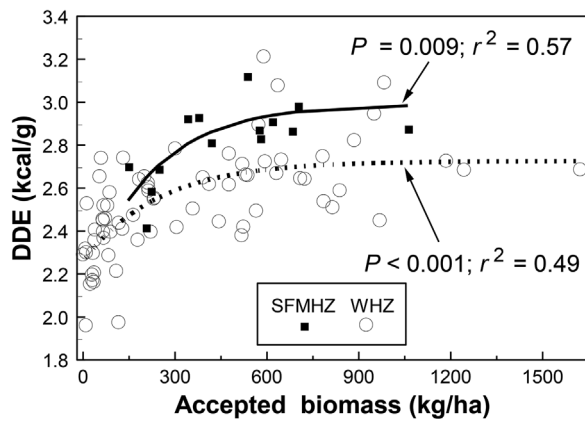


Figure 3. Non-linear relations of digestible energy (DDE) in elk diets and accepted biomass (biomass of neutral and selected species combined) by potential natural vegetation zones at Nooksack, Willapa Hills, and Springfield study areas in western Oregon and Washington, USA, 2000–2002 (adapted from Cook et al. [2016]). Potential vegetation zones are WHZ=western hemlock zone; SFMHZ=Pacific silver fir and mountain hemlock zones combined. The equation for the WHZ was $DDE = 0.47 \times (5.755 - e^{(-0.0041(AB))})$ and for the SFMHZ, $DDE = 0.92 \times (3.218 - e^{(-0.0052(AB))})$, where AB = accepted biomass in kg/ha.

the WHZ. In general, as abundance of the palatable, nutritious plants declined, elk increased consumption of the unpalatable forage. Because the unpalatable forage offered lower DE, this change in dietary composition substantially reduced DDE. When SB and NB were combined into a category referred to as accepted biomass (AB), DDE was asymptotically correlated with biomass of AB, with some differences evident among PNV zones (Fig. 3). This relationship forms the general basis of our nutrition model. Instantaneous intake rates of forage and DE generally failed to decline with biomass of AB, except at very low levels of AB, because elk increased consumption of avoided species, most of which provided significantly larger bite mass and thus relatively high intake rates of dry matter. In many cases, DDE levels were low enough to affect animal performance, despite relatively high instantaneous intake rates. Thus, DDE was a considerably more sensitive indicator of the nutritional value of plant communities to elk than was instantaneous intake rate of DE (Cook et al. 2016).

Data Analysis

Cook et al. (2016) developed equations to predict DDE as a function of forage biomass (with AB, NB, and SB as covariates) for the 3 study areas and PNV zones in which they sampled vegetation and elk diets (Fig. 4; Table 4). We expanded on that work by developing equations to predict biomass of AB, NB, and SB using covariates reflecting site characteristics (e.g., PNV zone, overstory canopy cover) and study area (Fig. 4). Cook et al. (2016) found no evidence that biomass of avoided species provided additional value in predicting DDE, and thus we did not develop equations for this forage biomass class. Finally, Cook et al. (2016) found no significant influences of season on DDE, and thus we used all data collected from late June to early November for nutrition model development, although we restricted the Westside habitat-use model to June–August because of hunting seasons (Rowland et al. 2018).

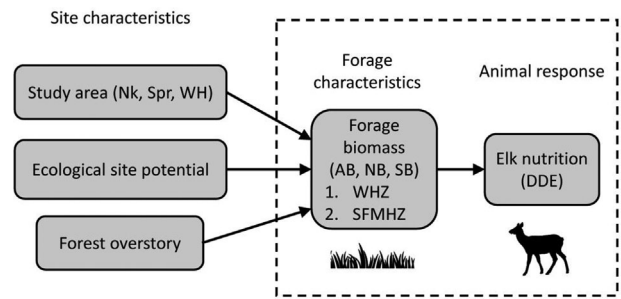


Figure 4. Illustration of basic components of the elk nutrition model for western Oregon and Washington, USA. The modeling process consisted of 2 basic steps to develop equations for 1) predicting biomass of forage based on forest overstory characteristics (e.g., overstory canopy cover, proportion of trees that are hardwood species) and ecological site potential as described for local potential natural vegetation (PNV) zones, and 2) predicting elk nutrition (dietary digestible energy [DDE]) based on forage biomass characteristics in 2 primary PNV zones of the region: western hemlock (WHZ) and Pacific silver fir–mountain hemlock (SFMHZ). Field data for both steps were collected by Cook et al. (2016), 2000–2002, at Nooksack, Washington (Nk), Springfield, Oregon (Spr), and Willapa Hills, Washington (WH) study areas. Equations to predict DDE based on biomass of 3 forage classes (AB = accepted biomass; NB = neutral biomass; and SB = selected biomass) within the 2 PNV zones were developed by Cook et al. (2016) from data collected using captive elk at the 3 study areas. Equations to predict forage biomass from selected site and forest overstory characteristics were developed herein. The final nutrition model combined both sets of equations into an overall model used to predict DDE across the Westside region.

To integrate analyses and summaries that we present here with DDE–elk performance relationships described by Cook et al. (2004:55), we modified their original 4 classes to create 6 DDE classes: <2.40, 2.40–2.58, >2.58–2.75, >2.75–2.83, >2.83–2.90, and >2.90 kcal/g (Table 2). Specifically, we halved the original good (2.75–2.90) and marginal (2.40–2.75) DDE classes to define the nutritional landscape of the Westside region more precisely. We defined basic DDE requirement as that level required for lactating elk to hold constant body fat levels over summer (~2.65–2.70 kcal/g of DDE; Cook et al. 2004) while raising a calf. Herein, we broadened this class by assuming that this basic requirement ranges from about 2.58 kcal to 2.75 kcal of DE/g of ingested food. However, this basic requirement inadequately provides for levels of autumn body fat of lactating elk, calf, and yearling growth rates, and early timing of breeding of which elk are capable if nutrition is excellent during summer (DDE >2.9 kcal/g; Table 2; Cook et al. 2004). We included analyses of DDE levels that not only satisfied the basic requirement but also those that exceeded the basic requirement.

Model development.—We developed equations to predict SB, NB, and AB based on overstory and other site characteristics using stepwise regression with backward elimination. In prior work, Cook et al. (2016) investigated a large number of potential overstory and site covariates, including their interactions; here, we reduced these into a more practical subset. Our first variable reduction step primarily reflected *a priori* expectations of importance but also reflected the reliability and coverage of data available in GIS for our entire mapping region. In light of this, we included 2 forest overstory variables (CC and proportion of overstory trees composed of hardwood species, the latter included because development of understory vegetation may be greater in hardwood forests than in conifer forests [Hanley et al. 2006]), PNV zone (to account for biophysical effects on

Table 4. Equations to predict dietary digestible energy (DDE) for elk based on biomass (kg/ha) of 3 forage classes by potential natural vegetation zones (Pacific silver fir and mountain hemlock zones [SFMHZ] and western hemlock zone [WHZ]) and 3 study areas (Nooksack [Nk], Willapa Hills [WH], and Springfield [Spr]) in western Oregon and Washington, USA (from Cook et al. [2016]).

Equation ^a	<i>n</i>	<i>R</i> ²	<i>R</i> ² _{adj}	<i>S</i> _{y.x} ^b	<i>P</i>
SFMHZ habitats, all seasons, all study areas DDE = 2.44 + 0.000889(NB) + 0.00308(SB) – 0.00000546(SB × NB)	14	0.56	0.43	0.134	0.036
WHZ habitats, all seasons, by study area DDE _{Nk} = 2.362 + 0.00108(NB) + 0.000504(SB) – 0.00000361(SB × NB)	19	0.49	0.39	0.223	0.015
DDE _{WH} = 2.278 + 0.00062(NB) + 0.00120(SB) – 0.00000172(SB × NB)	26	0.52	0.46	0.177	0.001
DDE _{Spr} = 2.300 + 0.00108(NB) + 0.00129(SB) – 0.00000418(SB × NB)	28	0.62	0.57	0.115	<0.001

^a Forage class codes (variable names) are NB = biomass (kg/ha) of neutral plant species (those plants that elk neither significantly avoided or selected), SB = biomass (kg/ha) of selected plant species (those plant species that elk significantly selected), and AB = biomass (kg/ha) of accepted species (SB and NB combined).

^b Standard error of the estimate.

vegetation composition, development, and plant chemistry [Franklin and Dyrness 1988, Henderson et al. 1992]), and study area.

We initially used the approach described by Stage (1976) to incorporate effects of slope and aspect on understory vegetation into our analyses. We found early in our analyses, however, that including slope and aspect in the regression equations resulted in a twofold overestimation of biomass on the steeper slopes of our study region. The fundamental problem was that most of the data were collected on flat and moderate slopes, and extrapolating results to the steeper slopes of the study area resulted in unrealistic estimates of forage biomass. Thus, we excluded slope and aspect from development of our final forage biomass prediction models.

We developed separate prediction models for each PNV zone because differences in vegetation and nutritional responses were greater among zones than among study areas (Cook et al. 2016). We also modeled differences within PNV zones among study areas using indicator variables. However, the MHZ and SFZ were well-represented in our sample only at Nooksack. Therefore, we pooled data across study areas for these 2 types, as was done for the DDE equations (Cook et al. 2016), and excluded indicator variables representing study areas for the MHZ and SFZ. Finally, because Cook et al. (2016) found no differences in DDE between the SFZ and MHZ, we pooled data, as they did, in these 2 high-elevation zones (hereafter referred to as SFMHZ).

Because forage abundance typically was nonlinearly related to CC (Cook et al. 2016), we used CurveExpert (CurveExpert 1.37; Daniel Hyams, Hixson, TN, USA) to identify functions to describe the nonlinear relations for our initial forage biomass-CC univariate analyses. This program provides multiple equations between response variables and covariates (1 covariate per run) and ranks each based on *S*_{y.x} (the standard error of the estimate). We selected the best formulations based on lowest *S*_{y.x}, and then reran these using PROC NLIN (Gauss-Newton method, SAS Institute 1988) to identify their statistical significance. If nonlinear versions were significant (*P* < 0.05) and provided lower *S*_{y.x} than linear versions, we considered the relationship to be nonlinear. However, we used nonlinear equation types (e.g., quadratic, logarithmic) that could be readily combined with other variables (proportion hardwoods, PNV) in stepwise multiple regression analyses for those CC-forage biomass relationships that were found to be nonlinear.

Using each biomass variable (SB, NB, AB) as dependent variables in separate analyses, we used stepwise regression with

backward elimination (PROC REG, SAS Institute 1988) to select a final model, based on a full model containing predictor variables for CC, hardwood proportion, PNV, and study area. We included the 2-way interactions between study area and CC but did not evaluate the interaction between proportion hardwoods and study area because stands with appreciable levels of hardwoods only occurred at Nooksack. We set the significance level for a variable to remain in the model at *P* = 0.15 for the stepwise analyses. We elected to use normal linear models for this analysis, preferring to avoid transformations of the response variables and thus retain data in their original units for simplicity and ease of application by users. We nevertheless evaluated residuals from the final models to identify 1) heteroscedasticity; 2) patterns in residuals that might flag inappropriate models; 3) non-normal distribution of residuals; and 4) deviation from 0 of residual means (Zar 2010). Our primary intent for using the residuals was an initial check that our modeling assumptions were met and provided reliable estimates of forage biomass.

We considered 10 independent variables in the stepwise regression analyses. Four of these were overstory canopy variables: percent CC and percent CC², where both were included to represent the nonlinear effect of CC, proportion hardwoods, and the interaction of CC and proportion hardwoods (the latter only applied in the WHZ because hardwood trees were largely absent from samples in the SFMHZ). We included 2 indicator variables representing the main effects of study area (STAR_{WH}, STAR_{Spr}, where STAR_{WH} = study area for Willapa Hills, STAR_{Spr} = study area for Springfield, and Nooksack was the reference study area). We also included the interaction of the indicator variables with CC and CC² (a total of 4 variables: STAR_{WH} × CC, STAR_{Spr} × CC, STAR_{WH} × CC², STAR_{Spr} × CC²).

As an additional check for consistent errors of our forage biomass prediction equations, we plotted predicted and observed biomass estimates for SB, NB, and AB for our entire data set in relation to stand age, and then fit a linear model to the predicted and observed values to estimate the slope coefficient of each relationship (slopes significantly different from 1.0 would indicate consistent errors in our prediction equations). To check for errors in our entire suite of DDE and biomass prediction equations, we compared observed versus 2 sets of predicted values of DDE for 1) early-successional stages and closed-canopy forests within study areas in the WHZ, 2) early-successional and closed-canopy forests across study areas in the SFMHZ, and 3) thinned and unthinned forest in WHZ with stand age limited to 20–60 years. We generated the first set of predicted DDE values from estimates of AB, NB, and

SB actually measured in each macroplot, and the second set of DDE values from predicted AB, NB, and SB for each macroplot. We calculated a paired *t*-test for each predicted-observed pair to identify errors from predicting biomass of our understory plant groups versus using actual data for each PNV-study area-thinning group.

Nutritional resource mapping.—To predict forage biomass and DDE levels for each 30-m × 30-m pixel across the Westside, we combined the DDE and associated AB, NB, and SB prediction equations into a GIS-based model (ModelBuilder, ArcGIS 9.3 and 10.0, Environmental Systems Research Institute, Inc., Redlands, CA, USA). We derived estimates for the forage biomass covariates from existing GIS layers (Appendix B, Table B2, available online in Supporting Information). Values of CC and hardwood proportion were from the Landscape Ecology, Modeling, Mapping, and Analysis (LEMMA) project (<http://www.fsl.orst.edu/lemma/main.php?project=nwfp&id=studyAreas>, accessed 20 Feb 2014; Appendix B). We used a digital elevation map (<http://ned.usgs.gov>) to calculate slope and aspect and obtained PNV data from the United States Forest Service (USFS; <http://ecoshare.info/products/gis-data/>, accessed 20 Feb 2014; Appendix B).

We used equations developed at Willapa Hills for prediction throughout the Coast Range including the Olympic Mountains west of Puget Sound and the Klamath Mountains at the extreme southwest portion of our study region (Fig. 1), those developed at Nooksack for areas in the northern Cascades, and those developed at Springfield for the western Cascades from the Washington-Oregon border to our southern boundary (Fig. 1). For agricultural areas, we used a constant DDE value of 2.83 kcal/g (National Research Council 1984), assuming that crops in this high-rainfall region would provide high-quality forage in most cases (crop types were variable, but pasture and hay lands, cereal grains, and orchards were common). We selected this DDE constant without specific knowledge of what crops were actually planted in a given year and locale, and thus it should be considered a rough estimate. However, agricultural areas were uncommon for most elk habitat-use modeling areas on the

Westside and composed only 8% of the Westside region (Wisdom et al. 2018a). We did not derive predictions of DDE for areas we assumed to be non-habitat for elk (e.g., suburban and urban areas, snow fields; Appendix B, Table B3).

We applied our DDE and forage biomass prediction equations developed from data collected in the WHZ and SFMHZ, without modification, in PNV zones for which we had no empirical data based on similarities of plant species composition between unsampled and sampled PNV types (Table 5). We chose appropriate crosswalks (i.e., assignment of unsampled zones to the 2 sampled ones) using vegetation descriptions from Franklin and Dyrness (1988) and Henderson et al. (1992). In general, we predicted forage biomass and DDE for unsampled PNV zones at low to moderate elevations using equations for the WHZ, and predicted biomass and DDE for unsampled PNV zones at relatively high elevations using equations for the SFMHZ.

Nutrition model evaluation.—We evaluated the performance of the nutrition model using 3 response variables of wild elk in relation to predicted DDE levels: 1) resource selection; 2) levels of autumn body fat of prime-aged (2–14 years of age) lactating elk; and 3) pregnancy rates of prime-aged lactating elk. Thus, our approach involved evaluating relationships between DDE predictions from the nutrition model developed at fine scales and higher-order responses of wild elk at broad scales. For the first, we calculated selection ratios (use/availability) for several categories (i.e., bins) of DDE, where a ratio >1 indicates selection and <1 indicates avoidance (Manly et al. 2002). We conducted this analysis simply to illustrate selection for different levels of DDE, without accounting for influences of other environmental covariates. Analyses of habitat use, in which nutritional resources and other covariates were combined in a multivariable framework, are presented by Rowland et al. (2018). For the 5 model development areas where location data were available from elk with global positioning system (GPS) collars (Table 1), we used 279,339 elk locations and a roughly equal sample of systematic points (284,110 points) in the same areas to calculate proportions used, proportions available, and selection ratios for each of 8 DDE bins. We divided the bins into

Table 5. Crosswalks, or assignments, of unsampled potential natural vegetation (PNV) zones in the Westside region, western Oregon, and Washington, USA, to the 2 sampled zones (crosswalked zones; i.e., WHZ, SFMHZ) used to predict elk nutritional conditions sampled in western Oregon and Washington, arranged in decreasing order from most to least abundant.

Original PNV zone	Crosswalked zone ^a	Area (ha)	% region
Western hemlock	WHZ	6,581,853	56.14
Pacific silver fir	SFMHZ	1,541,776	13.15
Douglas-fir	WHZ	1,077,866	9.19
Sitka spruce	WHZ	820,183	7.00
Mountain hemlock	SFMHZ	710,532	6.06
Grand fir	WHZ	332,700	2.84
Parkland	SFMHZ	315,591	2.69
Alpine	SFMHZ	87,805	0.75
White fir		81,385	0.69
Oregon white oak		74,567	0.64
Steppe	WHZ	57,244	0.49
Subalpine fir	SFMHZ	38,712	0.33
Grassland	WHZ	2,044	0.02
Ponderosa pine		1,290	0.01
Jeffrey pine		10	0.00

^a WHZ = western hemlock zone, SFMHZ = Pacific silver fir and mountain hemlock zones (combined). Empty cells are PNV zones masked from analysis owing to their dissimilarity to the 2 primary modeling zones.

increments that ensured all bins included at least ~5% of the landscape. We used bins of 0.05 kcal/g and truncated at DDE <2.45 kcal/g at the lower extent and >2.75 kcal/g at the upper extent. Equal-sized binning is a standard practice when calculating selection ratios or conducting analyses of predicted versus observed data for validation (e.g., Manly et al. 2002). This analysis was not a formal test of statistical significance; instead, we estimated selection ratios to identify the extent to which elk were associated with various levels of nutritional resources indexed by DDE. We calculated 90% confidence intervals (CIs) for the selection ratios by bootstrapping individual elk with $n=2,000$ iterations and identified CI endpoints using the percentile method (Manly 2006).

We used population-level estimates of body fat in autumn and pregnancy rates from 9 populations described by Cook et al. (2013) and Stussy (1993) to evaluate the relation between these 2 performance measures and percentage area by DDE class in each elk range (Fig. 1). All body fat and pregnancy estimates were for elk that raised a calf the previous summer based on presence of milk in the udder (Cook et al. 2013) because performance (body fat and ovulation dynamics) is considerably more sensitive to nutrition in summer and early autumn in lactating versus non-lactating elk (Cook et al. 2004, 2013).

Cook et al. (2013) estimated body fat using an arithmetic combination of ultrasound measures of thickness of the subcutaneous rump fat layer and a body condition score (scaledLIVINDEX; Cook et al. 2010) collected during at least 2 autumns (1998–2005) for each population. Stussy (1993) measured kidney fat index (Riney 1955) in 1988 and 1989 from hunter-harvested elk; we converted kidney fat to percent body fat using equations from Cook et al. (2001). The body fat estimates were obtained in November and early December with 3 exceptions: those at Springfield were sampled in early October (Cook et al. 2013), and those of Stussy (1993) for the 2 Siuslaw populations were obtained mostly in January (late Dec–Feb). Because body fat declines over winter and probably over autumn in these areas (Kohlmann 1999, Cook et al. 2013), we attempted to account for this decline using a conservative estimate of change of –0.5 percentage point/month in the Coast Range and –0.9 percentage point/month in the Cascade Range (Cook et al. 2013; i.e., –1 for Springfield and +1 for both Siuslaw populations) to be consistent with an average late-November sampling date for the other populations. Cook et al. (2013) determined pregnancy using rectal entry with ultrasound and confirmed non-pregnancy with pregnancy-specific Protein B of serum (Noyes et al. 1997), whereas Stussy (1993) inspected uteri of harvested elk to determine pregnancy. Research involving animal capture and handling was conducted in accordance with approved animal welfare protocol for the Starkey Experimental Forest and Range (#92-F0004; Wisdom et al. 1993) as reported in Cook et al. (2013, 2016).

To develop DDE estimates for each population using data from Cook et al. (2013), we defined population range boundaries with minimum convex polygons (MCPs) plus a 500-m buffer around the MCP boundary of elk locations from very high frequency (VHF) collars for many of the populations (Table 3; most elk sampled for body fat and pregnancy carried collars). R. Stussy (Oregon Department of Fish and Wildlife, personal

communication) provided population boundaries of sampled elk for both Siuslaw populations and D. Vales (Muckleshoot Indian Tribe, personal communication) provided boundaries for the Green River and White River populations (Table 3).

We calculated percentage of area within the population boundaries for 5 DDE classes that relate to performance measures of elk: >2.58–2.75, >2.75–2.90, >2.58, >2.75, and ≥ 2.90 kcal/g.

We then used logistic regression with a binomial link function (Hosmer et al. 2013) to predict pregnancy rates for the 9 elk populations, with the percentage of each population's range in each DDE class as the predictor. We computed r^2 values for logistic regression as described by McFadden (1974), and used 1 regression for each class to identify which level of DDE, if any, was related to pregnancy rate. We used the number of elk sampled in each population as an offset term to account for differences in sample size (Ramsey and Schafer 2012). We used linear regression on autumn body fat levels of each population with percent of area by DDE category to determine if any categories were related to body fat. We expected that areas with higher percentages of relatively good nutrition (DDE >2.75 kcal/g) would best predict body fat levels, whereas areas with somewhat lower nutrition (DDE >2.58–2.75 kcal/g) would best predict pregnancy rates (Cook et al. 2004).

We created a nutritional resource map for the entire Westside region, grouping DDE in 6 categories (Table 2), to provide an overview of the current (~2006) status of nutritional resources for elk and to compare nutritional resources among land owners. Based on this map, we calculated the percentage of area in each of the 6 DDE classes for the Westside region and for 7 ecological provinces as defined by Franklin and Dyrness (1988). We also calculated the amount (ha) and percentage of area by the 6 DDE classes for individual landowners, separated by PNV zones, and total area (ha) providing DDE >2.58 kcal/g to illustrate contributions by landowner. Landowners included the Bureau of Indian Affairs, Bureau of Land Management (BLM), USFS, National Park Service (NPS), states (primarily Washington Department of Natural Resources and Oregon Department of Lands), other government entities (counties, towns, and other miscellaneous), and private corporations (primarily forest management companies such as Weyerhaeuser Company, Plum Creek Timber Company, and Hancock Timber Resources Group). We excluded agricultural lands from these regional summaries.

We compared ambient temperature and precipitation levels during the summers for which vegetation and DDE data were collected (Cook et al. 2016) to 30-year averages (1981–2010) to evaluate potential deviations of our DDE and forage biomass data from long-term patterns. We determined temperature and precipitation levels for May–July and August–October for each study plot where captive elk were deployed during the year the plot was sampled and calculated the 30-year averages for these sites. We generated climate data with the ClimateWNA v4.62 software package (<http://tinyurl.com/ClimateWNA>) based on methodology described by Hamann et al. (2013).

RESULTS

Data from 346 macroplots from Cook et al. (2016) were available for model development: 276 macroplots in the WHZ, roughly

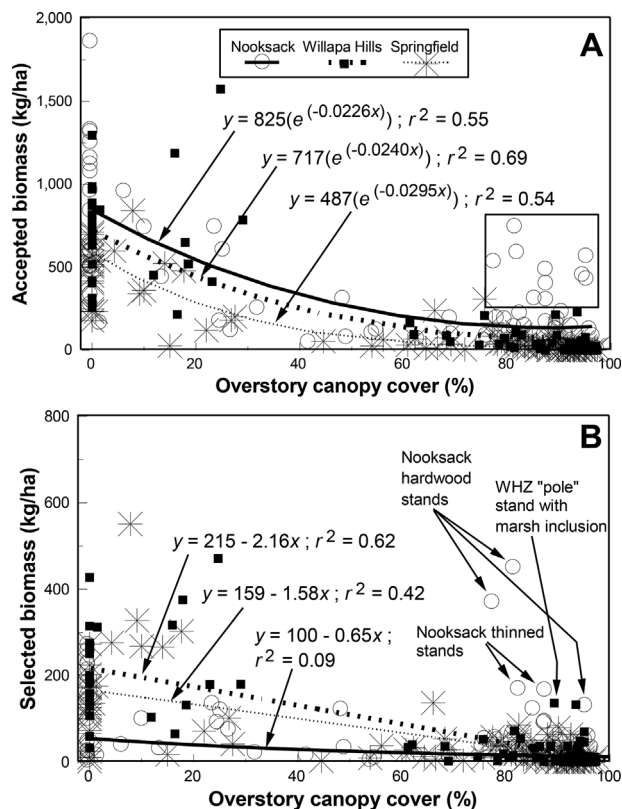


Figure 5. Relations of overstory canopy cover and biomass of accepted (A) and selected (B) plant species in the western hemlock zone (WHZ) at Nooksack, Willapa Hills, and Springfield study areas in western Oregon and Washington, USA 2000–2002 (relations between neutral biomass and canopy cover were virtually identical to those for accepted biomass and canopy cover; thus, only results for accepted biomass are displayed). Of the 10 anomalous points included in the square in the lower right corner in panel A, 8 were in hardwood stands, 1 in a thinned stand, and 1 in an untreated coniferous forest. Equations were significant at $P < 0.005$.

equally distributed among the Nooksack, Willapa Hills, and Springfield study areas; 33, 8, and 7 in the SFZ at the 3 areas, respectively; and 22 in the MHZ, all at Nooksack. We used captive elk in 32, 28, and 30 of the macroplots at the 3 study areas, respectively.

Model Development

Of the predictor variables examined, CC exhibited a strong relation with biomass of our 3 forage classes (AB, NB, and SB) in the WHZ at all study areas. For AB, the relation was nonlinear and was best fit overall with an exponential equation, with relatively high biomass levels occurring in early-seral stages with low overstory CC and low biomass levels under moderate and very high levels of CC (Fig. 5A). Modeling the nonlinear relationships using a quadratic function (CC and CC²) provided similar fit, and thus we opted to use a quadratic function to provide a simpler formulation for modeling the nonlinear relations in the subsequent stepwise regression. At very high levels of CC, several macroplots supported AB levels substantially in excess of that typically found in such stands. Nearly all of these were hardwood stands (inset of Fig. 5A). The general pattern for NB was nearly identical to that of AB; however, the relation between SB and CC was linear (Fig. 5B), with higher levels of SB in early-seral stands.

For our stepwise regression for data from the WHZ, analyses for both AB and NB included CC and CC², proportion hardwoods, and interactions of study area $\times$ CC and CC², with adjusted $R^2 \geq 0.65$ (Table 6). All independent variables included in both models were significant ($P < 0.002$). The regression equation for SB provided similar, though more variable results (adjusted $R^2 = 0.46$), except that the relation between SB and CC was linear rather than nonlinear (Table 6). Equations for all 3 forage classes reflected declining forage biomass as overstory CC

Table 6. Equations to predict biomass (kg/ha) of 3 forage classes for elk based on stand and forest overstory conditions by potential natural vegetation zones (Pacific silver fir and mountain hemlock zones [SFMHZ] and western hemlock zone [WHZ]) and 3 study areas (Nooksack [Nk], Willapa Hills [WH], and Springfield [Spr]) in western Oregon and Washington, USA.

Equation ^a	<i>n</i>	<i>R</i> ²	<i>R</i> ² _{adj}	<i>S</i> _{y,x} ^b	<i>P</i>
SFMHZ, all seasons, all study areas					
AB = 657.6 – 11.28(CC) + 0.0458(CC ²) + 553.06(HW)	70	0.71	0.70	187.51	<0.001
NB = 527.8 – 6.09(CC) + 590.49(HW)	70	0.73	0.72	151.39	<0.001
SB = 1/((0.00833 + 0.00062(CC)))	70	0.30	na ^c	68.45	<0.001
WHZ, all seasons, by study area					
AB _{Nk} = 707.3 – 13.93(CC) + 0.0731(CC ²) + 383.2(HW)	276 ^d	0.69	0.68	187.06	<0.001
AB _{WH} = 707.3 – 6.28(CC) – 0.0154(CC ²) + 383.2(HW)					
AB _{Spr} = 490.5 – 11.70(CC) + 0.0731(CC ²) + 383.2(HW)					
NB _{Nk} = 671.8 – 16.91(CC) + 0.1092(CC ²) + 268.1(HW)	276 ^d	0.66	0.65	158.76	<0.001
NB _{WH} = 477.4 – 3.90(CC) – 0.0151(CC ²) + 268.1(HW)					
NB _{Spr} = 308.5 – 7.59(CC) + 0.0473(CC ²) + 268.1(HW)					
SB _{Nk} = 80.1 – 0.66(CC) + 99.83(HW)	276 ^d	0.47	0.46	70.48	<0.001
SB _{WH} = 212.6 – 2.20(CC) + 99.83(HW)					
SB _{Spr} = 166.2 – 1.68(CC) + 99.83(HW)					

^a Forage class codes (variable names) are NB = biomass (kg/ha) of neutral plant species (those plants that elk neither significantly avoided nor selected), SB = biomass (kg/ha) of selected plant species (those plant species that elk significantly selected), and AB = biomass (kg/ha) of accepted species (SB and NB combined). Predictor variable codes are CC = overstory canopy cover (%); HW = proportion of stems in dominant canopy layer that are hardwood tree species (red and other alders [*Alnus* spp.], bigleaf maple [*Acer macrophyllum*], and paper birch [*Betula papyrifera*]).

^b Standard error of the estimate.

^c na = not applicable.

^d Separate equations developed from one regression analysis using indicator variables with interactions to provide separate coefficients, among study areas, for the intercept and both CC variables.

increased and modestly higher biomass in stands dominated by hardwood trees despite relatively high overstory canopy cover.

Equations produced slightly negative estimates (i.e., less than 0) of AB and NB at overstory CC $\geq 91\%$ and at CC $\geq 95\%$ for SB at Willapa Hills. Thus, we set any predicted value of forage biomass < 0 to 0 to eliminate negative predicted values.

In the SFMHZ, canopy cover again was the primary covariate for all 3 biomass classes. For AB and SB, the relation was nonlinear, but for NB, the relation was linear (Fig. 6A–C). The stepwise regression for AB included CC, CC², and hardwood proportion (Table 6) and accounted for 70% of the variation in AB. The stepwise regression for NB included CC ($P < 0.001$) and proportion hardwoods ($P = 0.002$) and accounted for 72% of the variation in NB (Table 6). The CC² term ($P = 0.262$) provided no improvement in either the S_{y-x} or adjusted R^2 . For SB in the SFMHZ, proportion hardwood was not significant ($P = 0.86$), and thus, our options for SB included only 2 equation types, the multiple regression formulation with CC and CC² and the nonlinear reciprocal equation originally identified using CurveExpert. Because of the lower S_{y-x} , we selected the reciprocal equation for prediction (Table 6).

Residuals from the prediction models, when plotted with overstory CC, generally indicated only modest heteroscedastic variances of each forage class across the range of CC, reflecting declining variance as CC increased (Figs. 5 and 6). We suspect that the greater variance at low CC reflected influences of factors that we did not include in the analysis, including site treatments just after logging, influences of vegetation communities that existed before logging (i.e., legacy influences), planting versus natural regeneration of conifers, time since logging, and other related factors. Overall, however, we observed no systematic patterns in the residuals (Appendix C, available online in Supporting Information), plots of residuals generally exhibited a normal distribution, and means of the residuals were ~ 0 , together suggesting the equations were robust. In addition, plots of observed and predicted values of our forage biomass types, though variable, illustrated good overall congruence across our data, and suggested that the equations were, in aggregate, unbiased (Fig. 7). Finally, estimates of DDE calculated directly from AB, NB, and SB field estimates in each macroplot using the DDE equations, and estimates of DDE calculated for each macroplot using predicted values of AB, NB, and SB, were consistently similar to observed DDE across high- and low-elevation forest zones, early-seral stages and closed-canopy forests among the study areas, and in thinned and unthinned stands (Fig. 8). We found no differences using paired t -tests between observed DDE and each estimate of predicted DDE by seral stage, PNV zone, nor study area ($P > 0.05$).

Based on the final model and vegetation data collected at each macroplot, predictions of DDE varied among PNV zones and defined a nutritional-succession sequence that illustrated substantial differences by seral stage and PNV zone (Fig. 9). These patterns illustrate the considerable nutritional value of early-seral communities, particularly those on moister soils and at higher elevations (Cook et al. 2016).

Westside Nutritional Resources for Elk

We identified 15 PNV types within our study area (Table 5). Of these, we considered 11 sufficiently similar to those sampled by

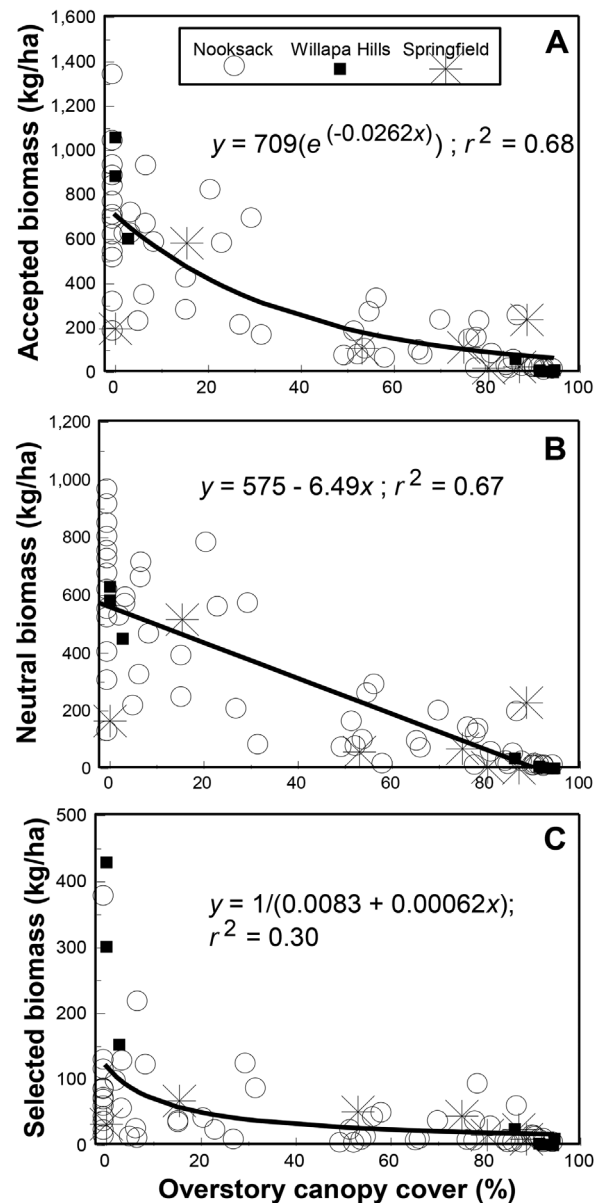


Figure 6. Relations of overstory canopy cover and biomass of accepted (A), neutral (B), and selected (C) plant species in Pacific silver fir and mountain hemlock potential natural vegetation zones at Nooksack, Willapa Hills, and Springfield study areas in western Oregon and Washington, USA, 2000–2002. Equations were significant at $P < 0.001$.

Cook et al. (2016) for direct application of our DDE and forage biomass equations (Table 5). This group included 4 PNV types that were permanently sparsely or non-forested: alpine, parkland, steppe, and grasslands. We used equations for SFMHZ for alpine and parkland types, and used equations for the WHZ for the steppe and grassland PNVs. The forest zones that we deemed too different for using our DDE and biomass equations were generally restricted to the extreme southern portion of our study area and were rare. The sampled PNVs, unsampled but crosswalked PNVs, and unsampled PNVs that we deemed too different for using our DDE and biomass equations composed 75%, 23%, and $< 2\%$ of our study area, respectively (Table 5).

Our Westside map of nutritional resources depicted vast landscapes of poor and below-requirement levels of DDE

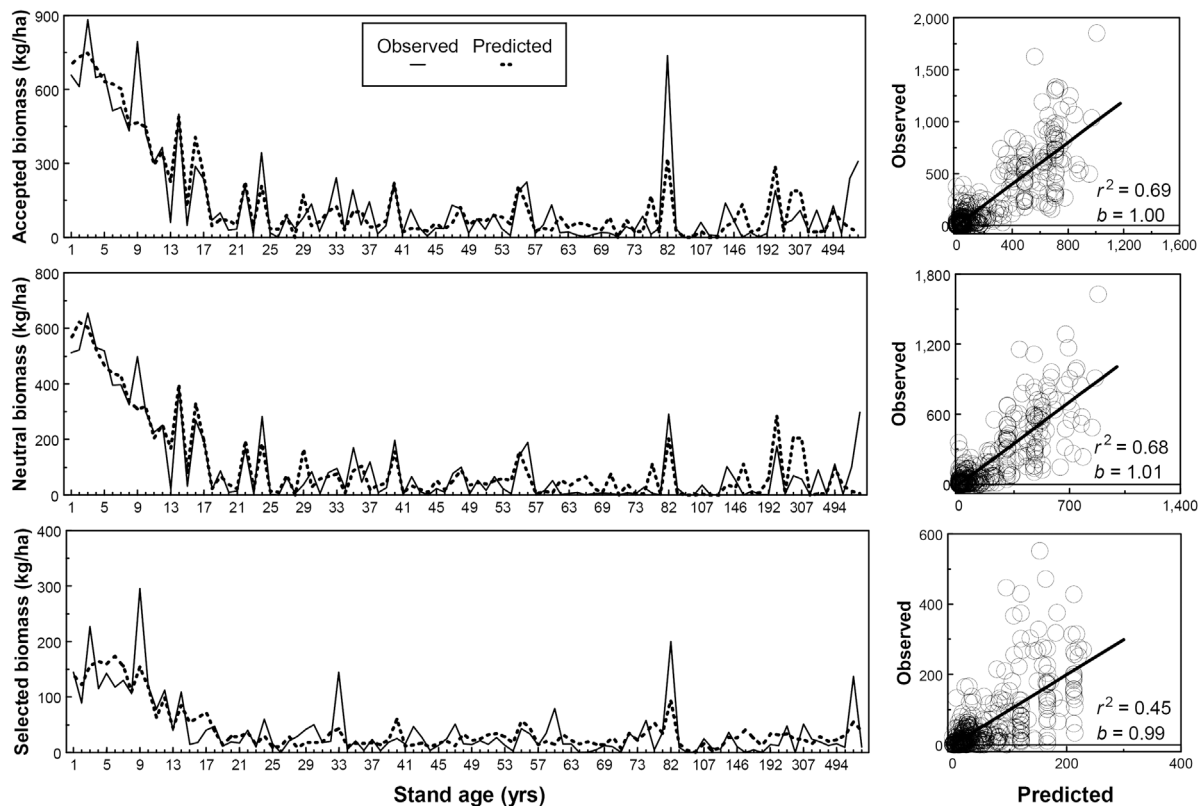


Figure 7. Observed and predicted values of accepted, neutral, and selected biomass of elk forage by stand age (left column). Cook et al. (2016) made predictions across the entire data set ($n = 349$) for vegetation sampling conducted at Nooksack, Willapa Hills, and Springfield study areas in western Oregon and Washington, USA, 2000–2002. We also present coefficients of determination (r^2) and slope coefficients (b) for predicted versus observed values of 3 classes of forage biomass (right column).

(≤ 2.58 kcal/g) throughout most of the region in 2006 (Fig. 10). In general, high DDE levels that met or exceeded requirement occurred only in high elevation, montane areas, most prominently in the Olympic Mountains and Cascades of Washington.

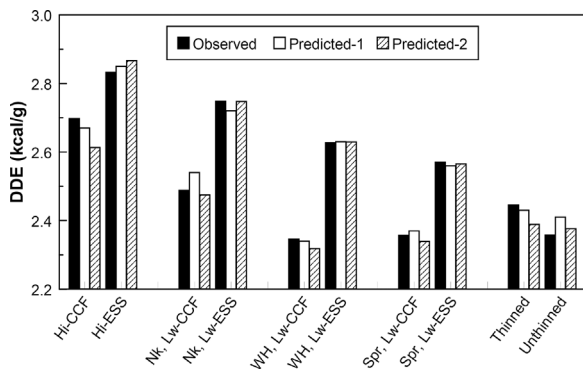


Figure 8. Means of predicted and observed dietary digestible energy (DDE) for elk by categories of potential natural vegetation, successional stage, and thinning for the Nooksack (Nk), Willapa Hills (WH), and Springfield (Spr) study areas in western Oregon and Washington, USA, 2000–2002. Codes are Hi = Pacific silver fir and mountain hemlock zones at high elevations across all study areas; Lw = western hemlock zone (WHZ) at lower elevations; CCF = closed canopy forests; ESS = early-seral stages; Thinned = thinned stands; and Unthinned = unthinned stands. Comparisons of thinned and unthinned were limited to stands in WHZ ranging in age from 20 to 60 years. Predicted-1 means were derived from DDE equations using actual field measures for accepted, neutral, and selected biomass of elk forage; predicted-2 means were derived from the same DDE equations but using predicted values of the 3 forage classes from the biomass prediction equations.

Nutrition Model Evaluation

Our analyses indicated strong correlations among modeled DDE levels, resource use, and performance. Elk with GPS collars exhibited strong selection for areas of relatively high DDE based on our selection ratio analysis. From 1 June to 30 August, selection ratios increased with increasing values of DDE (Fig. 11). Elk avoided areas with DDE < 2.55 kcal/g and selected for areas with > 2.60 kcal/g of DDE (Fig. 11).

Within the 9 populations used to evaluate relations between animal performance and DDE (Table 3), most of the various DDE levels exhibited high, although insignificant, correlations with pregnancy rate. Pregnancy rates of lactating elk were unrelated to percent area with DDE from > 2.58 to 2.75 kcal/g but significantly increased with increasing percent area with DDE > 2.58 kcal/g (Fig. 12C). Correlations were not significant between pregnancy rates and percent area with DDE > 2.75 kcal/g nor > 2.90 kcal/g (Fig. 12). The significant equation (i.e., with percent area with DDE > 2.58 kcal/g) seemed to simultaneously account for variation in pregnancy for populations with a significant percentage of area ($> 10\%$) with DDE > 2.75 kcal/g and for variation in populations generally lacking this higher DDE level. Our data also suggest that pregnancy rates > 0.9 occurred only on ranges with at least 10% of area with DDE > 2.75 kcal/g.

Autumn body fat of lactating elk exhibited a generally similar pattern (Fig. 13) but was increasingly correlated with percent area offering higher levels of DDE, in contrast to pregnancy rate. We concluded that the best regression for body fat was percent area providing DDE > 2.90 (although the regression for percent area with DDE > 2.75 was virtually identical; Fig. 13D and E).

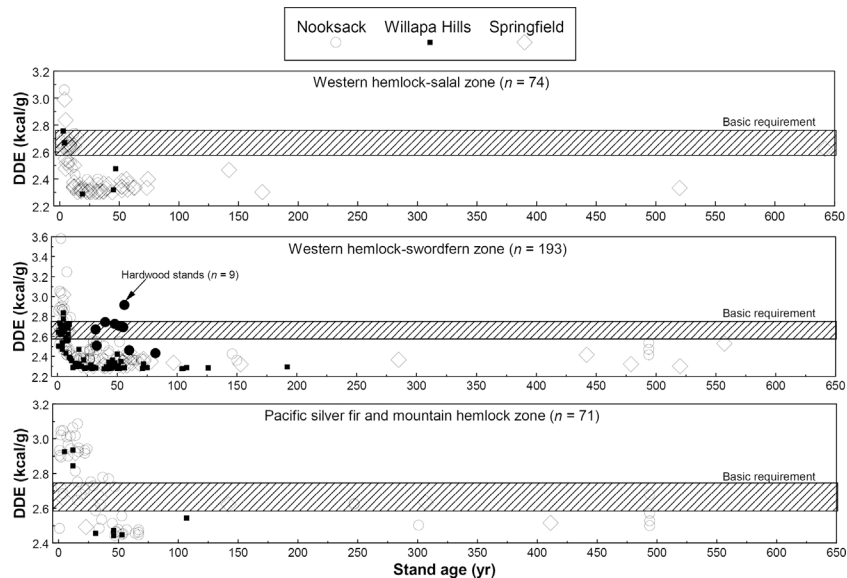


Figure 9. Estimates of dietary digestible energy (DDE) for elk in relation to stand age calculated from equations by study area and potential natural vegetation (PNV) zone at 3 study areas in western Oregon and Washington, USA, 2000–2002 (adapted from Cook et al. [2016]). Values of accepted, neutral, and selected biomass that predict DDE were measured at each field macroplot. The horizontal requirement line indicates the range of DDE levels (>2.58–2.75 kcal/g) needed by lactating female elk to hold constant body fat levels in summer (Cook et al. 2004).

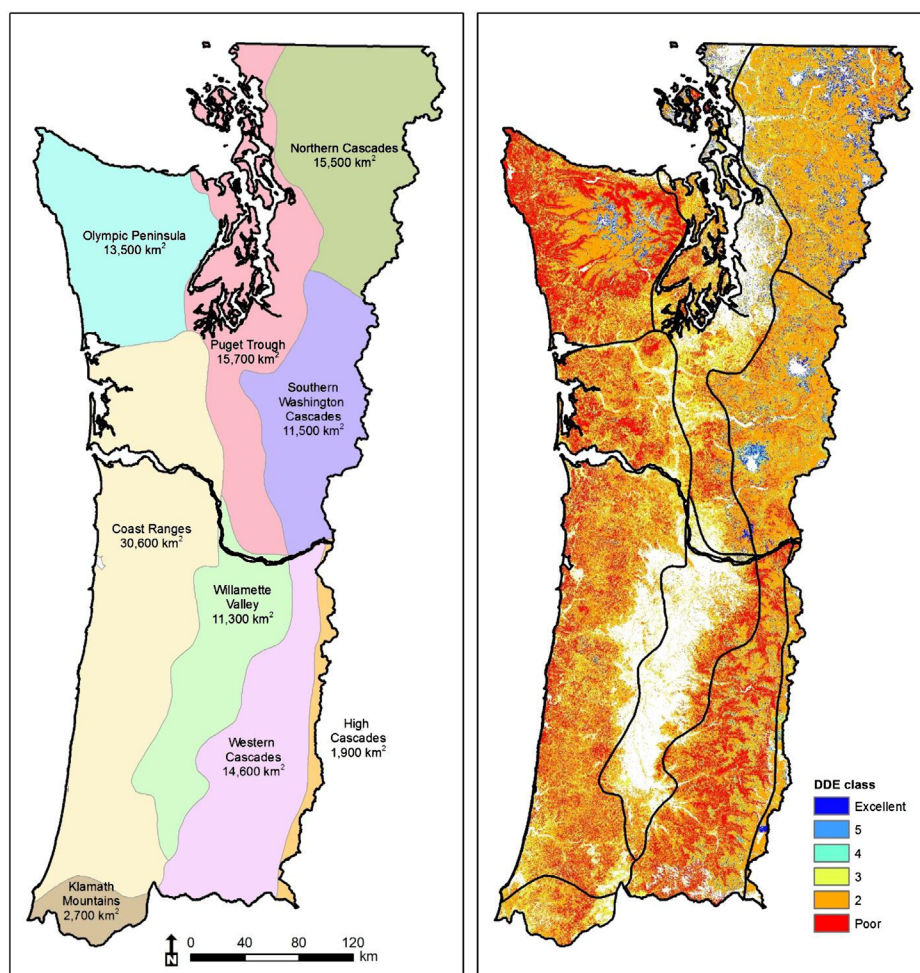


Figure 10. Ecoregions within the Westside region in western Oregon and Washington, USA (left panel). We also present predicted dietary digestible energy (DDE) for elk for 6 classes of DDE (<2.40 [1, poor], ≥2.40–2.58 [2], >2.58–2.75 [3], >2.75–2.83 [4], >2.83–2.90 [5], and >2.90 [6, excellent]). White areas denote agricultural lands and land cover types excluded as non-habitat (e.g., urban, suburban, and ice fields). Existing vegetation data used to predict DDE represent conditions in 2006.

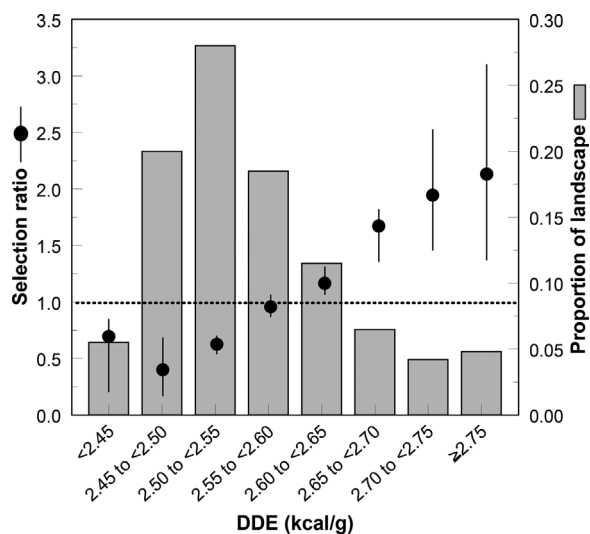


Figure 11. Selection ratios of wild elk equipped with global positioning system (GPS) satellite collars across 5 habitat-use modeling areas in central and western Washington, USA (2004–2009), and proportion of landscape by dietary digestible energy (DDE) classes. Selection ratios >1.0 suggest use greater than available; ratios <1.0 suggest use less than available. Vertical lines indicate 90% confidence intervals.

Regional Nutrition Patterns

Approximately 75%, 20%, and 5% of our entire region offered DDE levels below, around (>2.58–2.75 kcal/g), and in excess of basic requirement for lactating elk, respectively (Fig. 14). Among ecoregions, the greatest percentage of area providing DDE in excess of requirement was in the Cascades, with general declines from north to south from the Northern Cascades (15%), Southern Washington Cascades (11%), and Puget Trough (9%) in Washington to the Western Cascades in Oregon (5%). Areas with predicted DDE above requirement (>2.75 kcal/g) were virtually absent from the Coast Ranges and Willamette Valley ecoregions, and were largely absent except at higher elevations in the Olympic Mountains (Fig. 14).

Summaries of DDE levels among landowners were partitioned by PNW zones because land ownership tended to vary among zones (Fig. 15). Of the 5 major landowners in the WHZ, private, state, NPS, USFS, and BLM had 32.1%, 15.5%, 9.3%, 7.7%, and 6.5%, respectively, of area with DDE at basic requirement levels or better (>2.58 kcal/g). Private, NPS, BLM, USFS, and state had 39.4%, 34.2%, 30.9%, 29.4%, and 25.4%, respectively, of area with DDE at or above requirement in the SFMHZ. Across the entire study region, private lands provided 1.56 million ha of this DDE level, compared to 0.56 million ha on National Forest System lands, the second highest among other landowners (Fig. 16).

Temperature and precipitation patterns during the years DDE and forage data were collected were very similar to 30-year averages for May–July and August–October at Springfield and Willapa Hills, although the August–October period was drier than normal at Nooksack. During May–October, precipitation was 92% of the 30-year average (480 mm) at Springfield and was 96% of the 30-year average (505 mm) at Willapa Hills. At Nooksack, precipitation was 80% of the 30-year average (275 mm) during May–July and 29% of the 30-year average (450 mm) during August–October. Average daily temperature was virtually identical at Springfield compared to 30-year averages and about 1°C cooler over both summer periods at Willapa Hills and Nooksack.

DISCUSSION

Our results indicate that nutritional resources, as indexed by DE levels that elk acquire while foraging, were generally inadequate to satisfy nutritional requirements of lactating elk and their calves over vast areas of our Westside study region. Under these conditions, elk strove to compensate for inadequate nutritional resources by selecting areas that provided nutrition levels that satisfied or exceeded their basic requirements. We also found strong correlations between DDE levels available to elk and autumn body fat and pregnancy rates, supporting our prediction that significant links exist between nutritional resources and performance of elk populations across the vast landscape of our

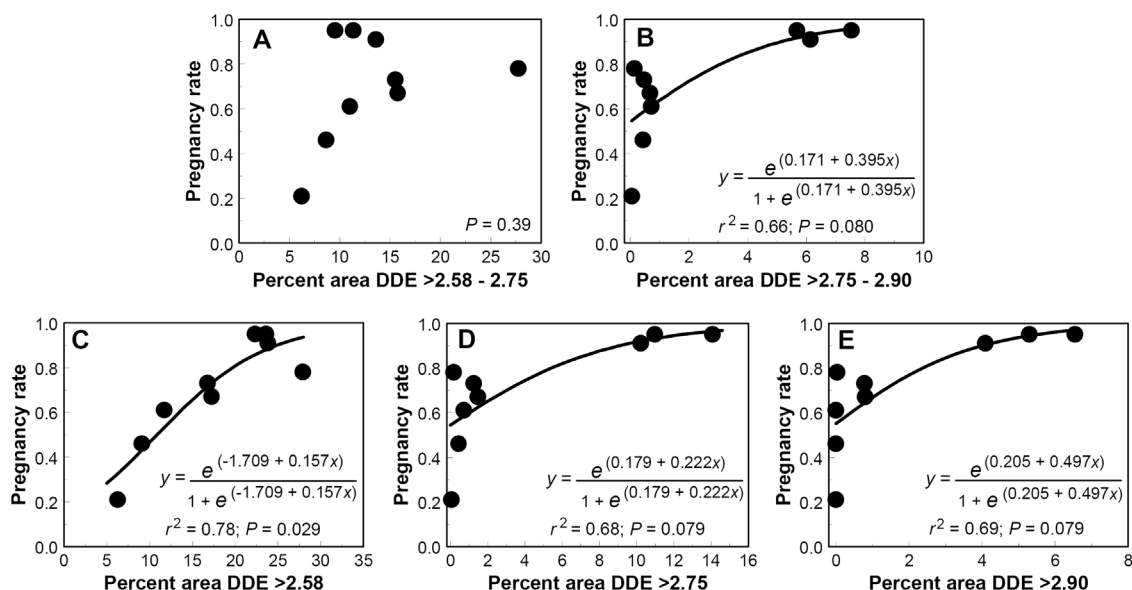


Figure 12. Relations between percent area in selected classes of predicted dietary digestible energy (DDE in kcal/g) and pregnancy rates of lactating wild elk in 9 populations in western Oregon and Washington, USA, 1998–2007. Note that r^2 values presented are pseudo- r^2 .

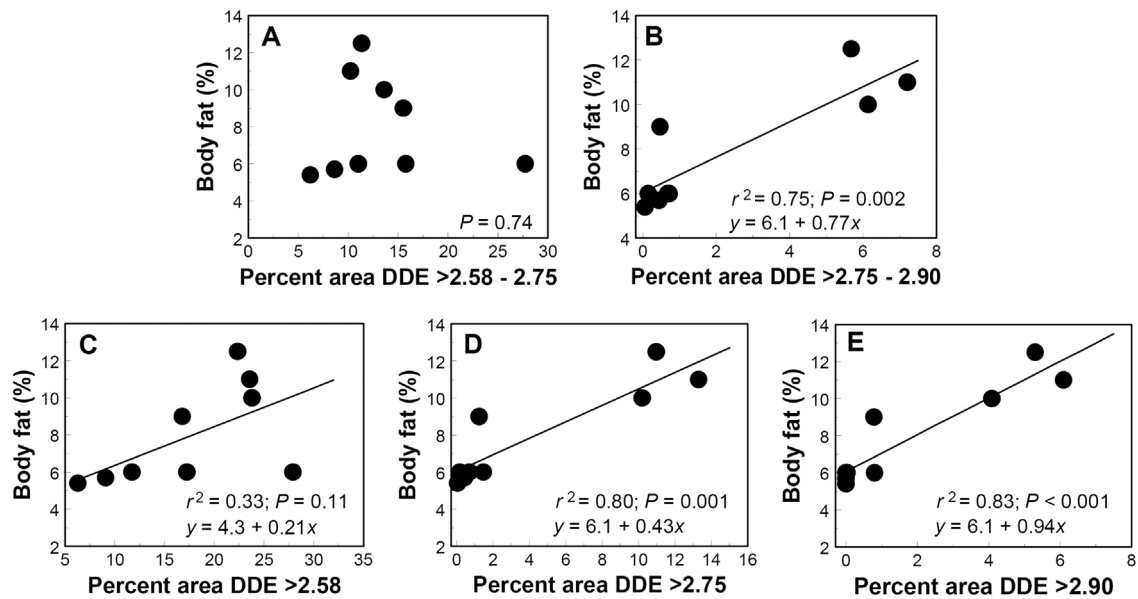


Figure 13. Relations between percent area in selected classes of predicted dietary digestible energy (DDE in kcal/g) and body fat in autumn of lactating wild elk in 9 populations in western Oregon and Washington, USA, 1998–2007.

study region. On ranges where nutritionally superior areas existed, autumn body fat levels and pregnancy rates were high, and where these areas were generally absent, performance suffered significantly. As such, our data strongly support 2 concepts pertaining to summer nutritional ecology and landscape planning. First, including summer nutrition as a key component of landscape models is required in the Westside region if these models are intended to adequately account for environmental influences on habitat use (Rowland et al. 2018), nutritional condition, and reproductive performance of elk. Second, data on elk nutrition dynamics collected at relatively fine scales can be effectively used to account for elk performance metrics at landscape scales in the Westside region. Evidence of the importance of nutrition in summer and early autumn for ungulates in western North America continues to increase (Dale et al. 2008, Cook et al. 2013, Hurley et al. 2014, Monteith et al.

2015, Proffitt et al. 2016), but our results are among the first to confirm that nutrition and foraging dynamics in summer measured at fine scales can be used to predict variation in higher-order population responses across broad, regional landscapes.

Largely because of the pioneering work of Trainer (1971), many studies evaluating nutritional condition and pregnancy rates of elk populations conducted in our study region have suggested that low nutritional condition in autumn and depressed pregnancy rates are widespread (Trainer 1971, Smith 1980, Harper 1987, Stussy 1993, Cook et al. 2013). We found that levels of DDE below basic requirement (≤ 2.58 kcal/g) composed 70–80% of our study region and 75% to $>90\%$ of the land base in the WHZ, which dominated across low to mid-elevations. Dietary DE levels that exceed the basic requirement (>2.75 kcal/g) were virtually non-existent in this zone, particularly on public lands. This bleak nutritional environment for elk in summer not only contributes to reduced elk performance but also may contribute to long-term shifts in elk distribution to areas providing better nutrition. Areas that provided substantial area of DDE >2.75 kcal/g (i.e., in excess of basic requirement) existed at relatively high elevations in the SFZ and MHZ, mainly in the mountains of the Olympic Peninsula and the Cascades (Fig. 14) in early seral stages with low overstory canopy cover. Here, opportunities for elk to acquire DDE in excess of basic requirement were substantially greater than in the WHZ at lower elevations.

Elk selected for areas providing at least basic requirement and showed strong selection for areas providing DDE in excess of basic requirement, supporting the prediction that elk recognize and actively seek these areas. Such strong selection undoubtedly is a strategy to avoid the negative fitness consequences of foraging at random (Moen et al. 1997)—the highest levels of pregnancy and body fat occurred on ranges with just 10–15% of area with DDE levels above basic requirement (Figs. 12 and 13), indicating the considerable ability of elk to exploit areas of superior nutritional resources within their seasonal ranges. Nevertheless, on ranges that provided $\leq 2\%$ of areas with DDE above basic requirement, performance was compromised, indicating elk were

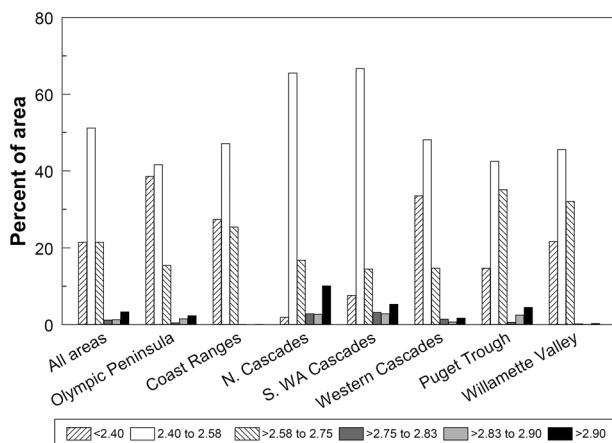


Figure 14. Percent area by ecoregion in each of 6 classes of predicted dietary digestible energy (DDE) for elk, with agricultural lands excluded, in western Oregon and Washington, USA. We excluded 2 peripheral ecoregions (Klamath Mountains and High Cascades) from summaries. Existing vegetation data used to predict DDE represent conditions in 2006.

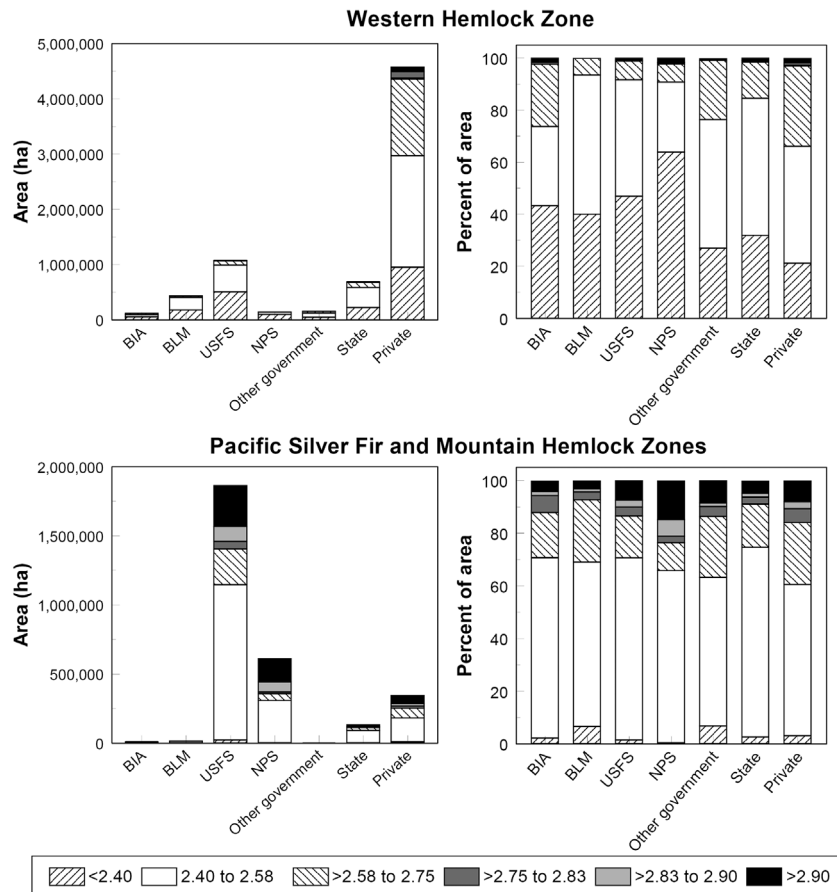


Figure 15. Total area and percent area by landowner in each of 6 classes of predicted dietary digestible energy (DDE) for elk in western Oregon and Washington, USA. We partitioned summaries by potential natural vegetation zones to reduce the influences of ecological conditions on results. Landowner codes are BIA = Bureau of Indian Affairs; BLM = Bureau of Land Management; USFS = United States Forest Service; NPS = National Park Service; Other government = state parks and local municipalities; State = Washington Department of Natural Resources or Oregon Department of Lands; and Private = non-governmental holdings (primarily private forest management companies). Predictions excluded suburban, urban, and agricultural lands. Existing vegetation data used to predict DDE represent conditions in 2006.

unable to fully compensate for poor nutritional resources on these depauperate ranges.

Our results supported our prediction that ranges that provided better nutritional resources during summer also supported greater autumn body fat levels and pregnancy rates of lactating elk. Similar results have been reported before, although across smaller land areas (Albon and Langvatn 1992, Hebblewhite et al. 2008, Proffitt et al. 2016). Perhaps what is most surprising in our study was the strength of the relationships between our 2 measures of performance (Figs. 12 and 13) and DDE levels despite the vast area of our evaluations and the relatively simple approach we used to quantify nutritional resources across elk ranges (i.e., percent of area offering different levels of DDE). In light of the strength of the relationships we found and the causal linkages between summer and early-autumn nutrition and animal performance that are becoming increasingly recognized (Hjeljord and Histol 1999, Dale et al. 2008, McArt et al. 2009, Hurley et al. 2014, Proffitt et al. 2016), we find little support for alternative explanations despite the fact that our analyses did not directly consider their possible influences. One alternative pertains to influences of weather and nutrition during winter. Detailed analyses by Cook et al. (2013) for our 9 populations indicated no significant influences of overwinter changes in nutritional condition, winter weather, or spring body fat on subsequent pregnancy rates and autumn body fat. This finding held for

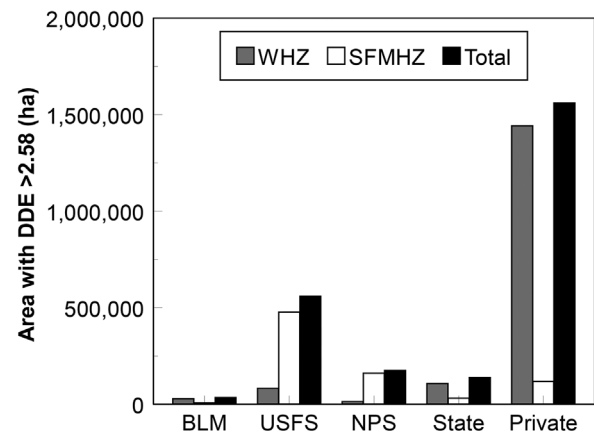


Figure 16. Total area with predicted dietary digestible energy (DDE) for elk >2.58 kcal/g by primary landowners in western Oregon and Washington, USA. Data are partitioned by the western hemlock (WHZ) and the Pacific silver fir and mountain hemlock (SFMHZ) potential natural vegetation zones. Landowner codes are BLM = Bureau of Land Management; USFS = United States Forest Service; NPS = National Park Service; State = Washington Department of Natural Resources or Oregon Department of Lands; and Private = non-governmental holdings (primarily private forest management companies). Predictions excluded suburban, urban, and agricultural lands. Existing vegetation data used to predict DDE represent conditions in 2006.

additional elk populations in areas of substantially harsher winter weather conditions. Based on analyses of all these ranges, they concluded that summer nutrition levels largely dictate both the apex and annual cycle of body fat levels (i.e., the summer-nutrition convergence hypothesis; Cook et al. 2013:29–30). Likewise, in controlled experiments, Cook et al. (2004) demonstrated that both pregnancy rate and autumn body fat in elk were driven by summer, not winter, nutrition, even for elk that exited winter with virtually no body fat. However, in ecological settings where winter weather is colder and snow accumulation is substantially deeper than the Westside region, and especially where inadequate summer nutrition limits body fat accretion and juvenile growth rates in summer, winter conditions certainly may influence performance of elk, especially over-winter survival.

Low levels of body fat and pregnancy might also be attributed to harassment by hunters (e.g., Davidson et al. 2012) and predators (e.g., Creel et al. 2007, but see White et al. 2011b, Boonstra 2013, Middleton et al. 2013b) that might either increase energy expenditure or force elk to forage in suboptimal vegetation communities. Wolves were absent but black bear and cougar were common in many areas of the region (Wisdom et al. 2018a). Studies on 2 populations in our sample (Green River and White River) demonstrated high levels of predation by cougars on elk calves ranging from 20% to 70% annually during the time that our nutritional condition and pregnancy data were collected (Washington Department of Fish and Wildlife 2002b). Yet these 2 populations had the second and third highest body fat levels and highest and third highest pregnancy rates of lactating elk in our study (Table 3). Displacement of elk during hunting seasons is increasingly documented, at least in relatively open areas that may offer less security cover than Westside landscapes (Conner et al. 2001; Johnson et al. 2005; Proffitt et al. 2009, 2010; Cleveland et al. 2012), but the strength of the DDE-body fat and pregnancy relationships (Figs. 12 and 13) suggests that such displacement accounts for little variation in performance of elk at broad scales in our region.

The relationships between animal performance and percent area in several DDE classes accorded well with our prediction based on the relationships between DDE and performance reported for elk by Cook et al. (2004). Only our regressions of percent of area providing DDE levels ≥ 2.75 kcal/g exhibited significant correlations with autumn body fat, agreeing with findings of Cook et al. (2004) that high levels of autumn body fat required over-summer DDE levels of approximately >2.9 kcal/g. The causal mechanism undoubtedly pertains to a declining rate of digestion and passage rates as DE content of forage declines. The overall effect results in a disproportionally large reduction in daily food intake and animal performance despite only modest declines in DE content of forage, a multiplier effect that is increasingly recognized (White 1983, Owen-Smith 2002, Cook et al. 2004, Hebblewhite et al. 2008).

Pregnancy rates were well-correlated to percent of area offering relatively high, but not necessarily the highest, levels of DDE, supporting our prediction and suggesting that nutrition levels required for successful breeding are lower than those needed to accrue relatively high levels of body fat. This relationship supports findings that calf and yearling growth rates, body fat accretion rates and subsequent autumn body fat, age-at-first breeding, and timing

of breeding were reduced at DDE levels that nevertheless supported high pregnancy rates (Cook et al. 2004; see Gaillard et al. 2000:384). The pregnancy-DDE relationships, however, may be more nuanced. Populations for which we had pregnancy data largely fell into 2 groups, those lacking areas ($\leq 2\%$ of area) providing DDE levels >2.75 kcal/g and those that provided at least a modest level (10–15%) above this DDE threshold. On those ranges with higher DDE, pregnancy rates exceeded 0.9 (Figs. 12D and E). On those lacking higher DDE, percent area providing DDE >2.58 kcal/g seemed well correlated with pregnancy rates, but rates in these populations were <0.8 (Fig. 12C). Because pregnancy rates peaked at 0.8 for those populations that contained virtually no areas of DDE >2.75 kcal/g (Fig. 12D), our data suggest an asymptotic upper limit to pregnancy rates as a function of the percent of area providing DDE >2.58 – 2.75 kcal/g. Larger sample sizes would be required to provide conclusive evaluation of this possibility.

We note several cautions for widespread use of these regressions, particularly for the relation between DDE levels and pregnancy rates. First, probability of breeding is a complicated physiological function reflecting body fat accumulated over the several months before breeding and, perhaps more importantly, nutrition at the time of breeding (Bronson and Manning 1991, Gerhart et al. 1997, Cook et al. 2013). Thus, in ecological settings where precipitation and temperature are considerably more variable during late summer and early autumn than in our region (e.g., DeYoung et al. 2018), the relationships between pregnancy and percent area by DDE class may be substantially more variable. Second, a more robust analysis would have been to quantify nutritional resources using metrics that included elk density on ranges for various DDE levels, rather than simply percent of area by DDE levels (Figs. 12, 13). Estimates of elk density were unavailable for most of our population ranges, and the markedly different sizes of elk ranges in our sample precluded evaluations based on absolute area, rather than percent of area. If elk populations were considerably larger, then a substantially greater percent of area with DDE >2.75 kcal/g may be required to support high levels of pregnancy and body fat.

In the following sections, we highlight a number of concerns, caveats, and justifications for the nutrition model and the approach we used to evaluate its reliability. First, the nutrition model is not a carrying-capacity model. For example, a vegetation community with 1,000 kg/ha of accepted forage may provide nutritional levels (DDE and intake rate of digestible energy) identical to those in a similar community but with 500 kg/ha of accepted forage. Clearly, the former would support more elk. Our model thus predicts the levels of nutrition that elk are likely to acquire under the conditions of the study, not the number of elk that potentially might be supported (see Cook et al. [2016] for additional comments regarding carrying capacity and density-dependent versus density-independent food limitations in our study region).

Second, instead of comparing predicted versus observed DDE using independent data as is normally the case for model evaluation, we compared higher-order responses of free-ranging elk (i.e., habitat use, body fat, and pregnancy rates at broad scales) with predicted DDE. We consider the latter approach to be a more useful evaluation strategy than the former (Babin et al. 2011) because it directly evaluates the ability of the model to address

higher-order, broad-scale processes despite the fine-scaled data used to develop the model. After all, it is the higher-order processes that really matter. If the nutrition model was invalid (i.e., unable to predict DDE with reasonable accuracy in areas beyond those where it was developed) or inaccurate (e.g., derived from GIS layers with insufficient accuracy or resolution for the predictor variables used), it is likely that 1) DDE predictions from the nutrition model would have been poorly related to nutritional resource selection (Fig. 11); 2) the DDE covariate in the habitat-use model (see Rowland et al. 2018) would have played a minor role compared to the other covariates in the model (other habitat and topographic features, anthropogenic disturbance); and 3) performance of free-ranging elk would have been poorly correlated to DDE (Figs. 12 and 13). Such was not the case for any of these criteria.

Third, many other measures of animal performance could have been used for evaluating the model, including those that largely reflect the direct influences of nutrition on performance (e.g., growth rates of juveniles and subadults, age at first breeding, timing of ovulation and breeding, neonatal calf size; Cook et al. 2004) and those that may or may not be directly influenced by nutrition (e.g., survival and recruitment rates, population trends). Adequately detailed data for these variables were not available for our analysis (see Cook et al. 2013). Further, the value of survival and recruitment rates as evaluation criteria for a nutrition model is potentially greatly confounded by many factors unrelated to nutrition (e.g., predation and hunting). We used body fat and pregnancy rates only for lactating females because their nutritional requirements are greater and thus their performance is markedly more sensitive to nutrition than are non-lactating adult females (Gerhart et al. 1997; Cook et al. 2004, 2013).

Fourth, captive ungulates have never before been used to develop large-scale nutrition models. Important disadvantages of using captive animals exist (e.g., high expense, concerns about disease, challenging field logistics, increasing regulatory limits on holding and transporting). However, their advantages are considerable, mainly by helping to reduce uncertainty about the relationships between vegetation attributes and nutrient content of diets and intake rate of nutrients over various time scales. This advantage is particularly true in structurally and floristically diverse plant communities, where bite mass, nutrient content, and plant defensive compounds may be highly heterogeneous among species and may have influences on elk foraging and nutrition that are difficult to predict (Cook et al. 2016). The detailed analysis of relationships between nutrition and vegetation characteristics using captive elk by Cook et al. (2016) explicitly identified those nutritional currencies that were most limiting, what vegetation characteristics accounted for these limitations, and those attributes of vegetation communities that nutrition modeling and habitat management programs should emphasize. That analysis greatly reduced the likelihood of a nutrition model constructed using nutritional currencies and vegetation characteristics that were not particularly relevant to elk in our ecological setting. Questions about the reliability of captive animals as proxies of wild animals have been answered with multiple ungulate species in a variety of studies (Yarrow 1979, Austin et al. 1983, Olsen-Rutz and Urness 1987, Spalinger et al. 1997). The considerable value of using captive animals for foraging studies was discussed by Hester et al. (2000) and Cook et al. (2016).

Fifth, there may be several vegetation community types in which our model is relatively inaccurate. The data collected in hardwood stands typically dominated by red alder (*Alnus rubra*) were mostly at Nooksack on very wet soils (Cook et al. 2016), but alder and other hardwood species also may dominate on substantially drier sites, particularly in the southern area of our study region (Franklin and Dyrness 1988). Thus the hardwood covariate may be less reliable in these drier settings. In addition, high elevation forest vegetation types that are substantially drier, less productive, and support markedly different plant composition than those sampled by Cook et al. (2016) exist in the southern Cascades (Franklin and Dyrness 1988). We expect that our nutrition model may overestimate DDE in these communities. Moreover, our assumption that overstory canopy cover was a suitable surrogate for tracking succession applies to early-seral stages soon after stand-replacing disturbance as conifers regenerate, but may not hold for mid-successional areas after partial harvests (e.g., commercial thinning). Our model may overestimate DDE in these stands. Our DDE equations probably are unreliable for treatments that alter chemical composition of plants (e.g., fertilization) or replace native vegetation with exotic species (e.g., seedlings of legumes on food plots).

Sixth, accuracy of our forage prediction equations depends on the accuracy of existing spatial data that we used as inputs (e.g., overstory canopy cover, PNV zone). Our analyses suggested errors due to inaccurate input data smooth out at broad scales, but errors may be of greater concern at relatively fine scales. The DDE prediction equations in the Westside nutrition model can be used at fine scales, for example to evaluate stand-level effects on DDE of different forest management prescriptions (Wisdom et al. 2018b). There are 2 methods of application that may differ in reliability. The first uses field measurements of overstory canopy cover and proportion of hardwoods from individual stands (≥ 1 ha in size) with the biomass and DDE equations to predict DDE for a variety of fine-scale applications. In contrast, using field-sampled estimates of forage biomass (e.g., by SB, AB, NB classes) to predict DDE should be more accurate than the former and may be most useful for evaluating effects of a variety of harvesting or silvicultural strategies that are not well-represented in the original data of Cook et al. (2016). For such stand-level evaluations, we recommend that Cook et al. (2016) and Rowland et al. (2013) be consulted.

Seventh, an important step for habitat evaluation and landscape planning models normally extrapolates either inferred or measured nutritional values (DDE in our case) at fine scales across large landscapes. Many approaches may inadequately account for underlying influences of ecological context and vegetation succession and thus may fail to provide a suitable basis to predict future conditions (Haufler 1994, Cushman et al. 2008). For example, land-cover classifications are often based on overstory species composition, but understory vegetation from which herbivores acquire nutrition may be poorly related to overstory species composition. Potential natural vegetation classification systems account for understory vegetation composition, and classification for a site does not change as overstory composition changes (Franklin and Dyrness 1988, Henderson et al. 1992). Further, PNV systems integrate the influences of soils, climate, and landform that can strongly influence vegetation composition, growth, and phenology, and all of these in turn influence forage biomass and quality. For these reasons, we

chose to use PNV systems on which to base our nutrition model (Haufler 1994). Large differences in plant composition, phenology, and elk nutrition that existed among PNV zones (Cook et al. 2016) attested to the value of such a classification system for our purposes. Nevertheless, the process of extrapolating fine-scale forage and nutrition data across broad landscapes in ways that are relevant to foraging herbivores needs further evaluation, particularly for areas where high quality, ecological-based vegetation mapping systems are lacking.

Finally, temperature and precipitation patterns during the original data collection (Cook et al. 2016) also could be a source of uncertainty about the veracity of the nutrition model. Weather patterns when the data were collected were very similar to long-term averages, except for precipitation in late summer at Nooksack, thereby suggesting that the nutrition model should represent most years within the region. Nevertheless, the reliability of the model in the face of climate change eventually may become an issue. By 2050, temperatures at least in western Oregon are expected to increase 1.7–3.9°C, annual precipitation is expected to increase slightly, whereas summer precipitation may decline, and the frequency of drier, hotter summers may increase (Dalton et al. 2017). For ungulates, we would predict milder winters, earlier initiation of forage growth in spring, and earlier cessation of growth in summer, thereby reducing forage quality and increasing nutritional limitations in summer (Hebblewhite et al. 2008, Post and Forchhammer 2008). Forage quality levels of the recent past are implicitly included in the nutrition model, providing considerable advantages for nutritional resource evaluations under current climate (i.e., detailed forage quality and quantity surveys are not needed to use the model). However, this advantage renders the model invariant to changing climate, and changes in summer climate may reduce the reliability of the model for the Westside region. Nevertheless, we posit that the model should predict at least relative nutritional differences among PNV zones and successional stages with reasonable accuracy despite at least some changes in climate because many of the differences in nutritional responses among these were due to strong differences in plant composition and differences in precipitation and temperature along elevation gradients. We base this conclusion on the assumption that species composition and elevational influences on temperature and precipitation will largely remain unchanged over the medium term (≤ 2050).

The science associated with incorporating nutritional ecology of ungulates into habitat evaluation and landscape planning models has been relatively slow to develop. Past use of various untested surrogates of nutrition is increasingly criticized (Searle et al. 2007). Assessing only forage quantity excludes the influences of forage quality and would certainly be inadequate for modeling elk nutrition in the Westside region. Even the assumption that estimates of forage quality and quantity combined provide a reliable means to predict dietary quality and nutrient intake rates of herbivores is generally untested. The strength and consistency of explicit relationships between forage and nutritional outcomes largely remain unevaluated for chemically and structurally complex plant communities (Spalinger and Hobbs 1992, Cook et al. 2016). Finally, measures of nutrition variables most suitable for indexing nutritional value also are uncertain. That DE is more important in

ungulate nutritional ecology than protein is supported by others (Skogland 1991, Illius and Gordon 1999, Searle et al. 2007), but debate about protein versus DE nevertheless is ongoing (McArt et al. 2009), and their relative importance may vary among ecological settings. Also, instantaneous and daily intake rates of food or nutrients are classically considered for relating forage conditions to higher-order processes of animal performance and distribution (Fryxell 1991, Spalinger and Hobbs 1992, Searle et al. 2007, Babin et al. 2011).

For our ecological setting, where overall forage quality tended to be relatively low and total forage biomass quite high, forage intake rates were largely invariant across a wide variety of ecological and successional states (Cook et al. 2016). Thus, the most suitable nutritional currency for modeling nutritional resources may strongly depend on characteristics of soils, climate, and vegetation among ecological settings. By using captive elk to identify appropriate covariates and nutritional currencies for modeling, it should be well-tailored to the Westside region. However, the model may not be robust in different ecological settings. If a similar nutrition model is desired for other areas, choices will have to be made between the reliability that using captive animals offers and other approaches that may not as effectively index nutritional resources.

MANAGEMENT IMPLICATIONS

Our results identified a key role of active habitat management for improving nutritional resources across Westside landscapes. Ecological conditions within PNV zones largely set the lower and particularly the upper limits of DDE, but disturbance and succession strongly influenced DDE levels within these limits. Levels of DDE that satisfied or exceeded basic requirement were restricted almost entirely to early-seral stages following stand-replacing disturbance (Fig. 9), confirming the importance of these communities for elk nutrition (Hett et al. 1978; Merrill 1987, 1994; Jenkins and Starkey 1996; Hutchins 2006). Extent of benefits accrued from vegetation management will vary by elevation. Duration of early-seral areas supporting high levels of DDE was much shorter in the WHZ (15 yr) than in the higher elevation PNV zones (~ 30 yr in the SFMHZ; Fig. 9). Thus, over the long term, a more aggressive habitat improvement program would be required in the WHZ than in the higher elevation zones to maintain nutritionally adequate landscape mosaics for elk and to support productive elk populations for substantial hunting opportunities.

The primary type of disturbance reflected in our data was clearcut regeneration harvest, although thinning also was evaluated in the WHZ by Cook et al. (2016). Dietary DE levels were modestly elevated but remained below basic requirement in thinned stands, and others reported that vegetation responses to thinning are variable (Alaback and Herman 1988, Thomas et al. 1999) and provide little improvement in forage for elk (Jenkins and Starkey 1996). In the SFMHZ and particularly in the MHZ, the slower rate of succession and the greater dominance of palatable plants even under forest canopies suggest that thinning probably will result in greater increases in DDE that persist longer than in the WHZ (Cook et al. 2016). The management examples provided by Wisdom et al. (2018b) also demonstrate the superior nutrition produced from clearcut regeneration harvest versus responses to light commercial thinning.

Prescribed burns and wildfire were not evaluated by Cook et al. (2016), but we predict that nutritional responses after stand-replacing wildfires would be similar to those after clearcut logging, based on early-seral vegetation responses after wildfire described by Franklin and Dyrness (1988; see Proffitt et al. 2016). We also speculate that under-burns in thinned stands may significantly improve forage for elk compared to thinned stands that have not been burned, by reducing unpalatable evergreen shrubs and ferns, and increasing growing space for palatable plant species.

As a result of the Northwest Forest Plan (USDA Forest Service and USDI Bureau of Land Management 1994*a, b*), constraints to forest management on public lands may represent significant opportunity costs for production of elk. Our summaries indicate private landowners (primarily forest products companies) provided substantially more land area with levels of nutrition that at least satisfy basic requirement (i.e., >2.58 kcal/g): 32% in the WHZ on private lands mainly due to clearcut logging versus 7% of area of federal public lands due to cessation of timber harvest beginning by the mid-1990s (Wisdom et al.

2018*a*). Within PNV zones at higher elevations (SFMHZ), the percent area providing DDE >2.58 kcal/g of nutrition was less divergent among the landowners (39% on private lands and 29–34% on federal lands). These differences were primarily due to overall higher DDE, slower forest succession, and presence of non-forested alpine vegetation in some areas (for which our model predicted very high levels of DDE). Our data suggest that stand-replacing disturbance provides important opportunities to improve nutritional resources significantly even in the driest communities in the WHZ, although the greatest opportunities for providing high nutrition are in the wetter, cooler communities in the WHZ and particularly in the SFMHZ at higher elevations. The USFS is the predominant land manager of these high-elevation lands (Fig. 16) with greatest potential to support productive elk populations. Where opportunities exist for forest management on high-elevation ranges, these should be carefully planned to effectively bolster their nutritional value for elk, if providing good habitat for elk is a management priority.

Linking Nutrition With Landscape Features in a Regional Habitat-Use Model for Elk in Western Oregon and Washington

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INTRODUCTION

Studies that reveal habitat selection and use by wildlife—especially large mammals—are foundational for understanding their ecology and management, especially if predictors of use can be linked to demography or fitness. Many ungulate species not only serve societal needs as game animals or tribal foods (McCabe 2002, Vales et al. 2017) but also affect native vegetation and agricultural crops because of their large body size, diet choices, and extensive distributions (Hobbs 1996, Schoenecker et al. 2004, Wisdom et al. 2006). Improved understanding of habitat relationships of large mammals, such as elk, can inform current wildlife conservation and management (Fortin et al. 2008) and provide a framework for evaluating future hypothesized environmental conditions (e.g., under climate change; Hebblewhite 2005, Durner et al. 2009). Habitat studies are often fraught with challenges, from inconsistent terminology to choosing research designs and metrics that properly evaluate use or selection (Garshelis 2000, Gaillard et al. 2010, Morrison 2012). We adopt a niche-based definition of habitat (i.e., functional

habitat) that includes the resources and environmental conditions that lead to a given level of performance (Hutchinson 1957, Hall et al. 1997, Gaillard et al. 2010). We chose to model intensity of habitat use, rather than habitat selection, in part because it captures not only the probability of selection but also how often a specific resource is encountered (Lele et al. 2013; see section Methods).

A key challenge in managing broadly distributed species like elk is to correctly identify the ecologically relevant variables that most influence habitat use. These variables can be integrated to generate landscape-level predictions of how animal distributions respond to different patterns of land management and habitat attributes over time and space. Habitat characteristics that drive spatial and temporal patterns of elk distributions have been studied since the 1970s, initially in response to widespread timber harvest, livestock grazing, and road construction across landscapes supporting important elk habitat in the western United States (Leege 1984, Lyon et al. 1985). Biologists used these findings to develop a diverse suite of elk habitat models (e.g., Lyon 1979; Thomas et al. 1979, 1988; Wisdom et al. 1986; Roloff 1998; Unsworth et al. 1998).

Contemporary analytical approaches to modeling habitat use and resource selection (Manly et al. 2002, Johnson et al. 2006, Long et al. 2008, Nielson and Sawyer 2013), coupled with the increasing availability of broad-scale spatial data and large telemetry data sets (Frair et al. 2010), have facilitated development of more advanced, spatially explicit models of elk

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distributions and habitats (e.g., Johnson et al. 2000, Coe et al. 2001, Boyce et al. 2003, Sawyer et al. 2007, Proffitt et al. 2010). Moreover, previously unavailable predictors such as phenology-based metrics of greenness (Hebblewhite et al. 2008, Bischof et al. 2012) or LiDAR-based measures of forest structure (Ewald et al. 2014, Lone et al. 2014) have augmented more traditional model covariates. Research elucidating combined effects of gray wolves and human disturbance (Proffitt et al. 2009) or wolves and climate change (Hebblewhite 2005) on elk further demonstrate the expanding complexity of elk habitat studies. Despite widespread application of elk habitat models in land-use planning (Edge et al. 1990, USDA Forest Service 1990, Christensen et al. 1993), few have been validated with independent data (but see Rowland et al. 2000, Roloff et al. 2001, Benkobi et al. 2004, Sawyer et al. 2007, Coe et al. 2011). Rigorous evaluation of model performance is essential (Johnson 2001, Shifley et al. 2009, Morrison et al. 2012), especially for models guiding public land management decisions that may be challenged in court or applied across thousands of hectares.

A limitation of many prior habitat models for elk and other wildlife species is the appropriate inference space for model application (Morrison 2012). Studies of habitat use or resource selection by animals commonly rely on a single sample of animal locations obtained via GPS or VHF technology. Although some studies span years, most are designed to focus on a specific management question within a limited area, and thus are viewed in isolation. For example, Sawyer et al. (2009) monitored changes in mule deer (*Odocoileus hemionus*) distributions in response to development of a gas field, McDonald et al. (2006) identified how northern spotted owls (*Strix occidentalis caurina*) selected nest locations on a large tract of privately owned land, and Goldstein et al. (2010) tracked brown bears (*Ursus arctos*) on the Kenai Peninsula, Alaska to evaluate the potential for human recreation to disturb denning females. Inferences from these single studies are constrained in both space and time; very few studies focus on estimating habitat use across larger populations at spatial extents that cross multiple jurisdictional boundaries.

Similarities among studies in how animals were sampled, data collection protocols, and data quality, however, may allow for synthesis of information on a larger scale. For example, Durner et al. (2009) combined over 19,000 polar bear (*U. maritimus*) locations recorded over 22 years from 8 of 19 polar bear subpopulations to investigate the potential for global climate change to influence the loss of optimal polar bear habitats. In another unique study, Guldmond and Van Aarde (2008) conducted a meta-analysis on 21 studies published from 1961 to 2005 to evaluate effects of elephants (*Loxodonta africana*) on woody vegetation in savanna landscapes.

We can develop more precise estimates of the size of an effect by examining multiple investigations, rather than a single study (Borenstein et al. 2009). Analysis of data from multiple studies with similar data collection techniques, albeit different primary goals, also may reduce dependence on individual studies and identify general animal-habitat relationships that are robust across the sampled populations (Johnson 2002, Borenstein et al. 2009) or that vary along geographical gradients (Fortin et al. 2008). Similar to Durner et al. (2009), we sought to use data from several disparate telemetry studies in a meta-analysis approach to

develop a model that identified commonalities in habitat-use patterns across a large geographic range for a single species. However, unlike Durner et al. (2009), we also sought to recognize the hierarchical nature of the animal location data (thousands of locations from dozens of animals within several model development areas) in the variable selection and model estimation process by adopting a 2-stage approach that modeled patterns of use within modeling areas and then summarizing use at a regional level (Fieberg et al. 2010). Further, we recognized that most regional habitat-use models cannot be simultaneously general, realistic, and precise. We chose to focus on generality and realism in our approach, rather than precision (Levins 1966). Such an approach emphasizes qualitative, versus quantitative, results, and is thus more widely applicable within the intended inference space.

The biological hypothesis and predictions guiding our habitat modeling objectives were as follows. We hypothesized that elk habitat use during summer is driven by a suite of interacting covariates related to energy balance: acquisition (e.g., nutritional resources, juxtaposition of cover, and foraging areas), and expenditure (e.g., proximity to open roads, topography). Among covariates, we predicted that nutrition and human disturbance would function as key drivers of elk distribution because of the preponderance of support from the literature on their role in influencing habitat use by elk. Specifically, we predicted that elk would seek areas offering the best nutritional resources but avoid roads because of associated human disturbance and avoid areas far from cover-forage edges because of their preference for foraging sites with secure patches of cover nearby. We also predicted that sites of similar nutritional value might differ in their realized use by elk because of environmental constraints such as human disturbance or rugged terrain. We describe a structured, multi-step process to develop and validate new habitat-use models for elk in western Oregon and Washington (hereafter Westside), using multiple telemetry data sets. We then report results of applying this process, interpret modeling results, and describe potential implications for managing elk.

Given our overarching hypothesis about elk habitat use and its relation to energy balance, our primary objective was to construct and validate a summer, landscape-scale model of habitat use for elk across Westside land ownerships that integrated ecologically relevant covariates characterizing nutrition, human disturbance, vegetation, and physical conditions. The covariates considered were directly related to elk habitat use (e.g., elk dietary digestible energy), rather than surrogates that could be more difficult to manage or interpret (Sawyer et al. 2007, Wisdom et al. 2018a), such as normalized difference vegetation index (NDVI; Hebblewhite et al. 2008, Pettorelli et al. 2011). Our emphasis on summer habitat use was driven by the inadequacy of many Westside vegetation communities to provide sufficient nutritional resources to meet maintenance requirements of lactating elk during summer (Cook et al. 2013, 2016) and the potential to evaluate and address this limitation by developing nutrition and habitat-use models (Cook et al. 2018, Wisdom et al. 2018a).

A second objective was to explicitly incorporate mechanistic covariates reflecting concepts of energy balance (Wisdom et al. 2018a). Several studies of elk have demonstrated avoidance of humans and predators, which can affect foraging dynamics and

resource acquisition (Frair et al. 2005, 2008; Muhly et al. 2010, 2013; Ciuti et al. 2012a, b; White et al. 2012), as well as movement rates (Hurley and Sargeant 1991, Wisdom et al. 2005a, Naylor et al. 2009). A third objective was to develop a robust regional habitat-use model, an outcome possible only if patterns of elk habitat use were consistent across the range of conditions found in the Westside model development areas. Fourth, we wanted to develop a desktop GIS tool for managers to 1) identify locales where nutritional resources and elk use are relatively high or low and 2) evaluate relative improvements in nutritional resources and elk use as a result of management actions at multiple scales and land ownerships (see Rowland et al. 2013, Wisdom et al. 2018b).

METHODS

For the Westside elk project, we modeled intensity of habitat use by evaluating elk locations in relation to habitat features (covariates; Gaillard et al. 2010, Nielson and Sawyer 2013), which is considered an analysis of habitat use. This analysis differs somewhat from an analysis of habitat selection (Manly et al. 2002), which Lele et al. (2013:1185) defined to be strictly a “binary [behavioral] decision, with outcomes of use or non-use of a resource unit.” Such behavioral decisions result in patterns of intensity of use of a habitat or resource unit. The intensity of use depends not only on the probability of selection but also on the frequency with which a specific resource unit will be encountered (Lele et al. 2013). Modeling habitat use along a continuum can provide more information about the relationships between habitat characteristics and probability of use by the animal. This modeling approach reveals where animals are on the landscape and the relative amount of time spent by them in each sampling unit, rather than presence or absence of animals as typically reported in use-availability studies (Manly et al. 2002, Nielson and Sawyer 2013). The habitat-use approach met our primary objective of modeling distributions of elk across land ownerships of the Westside region. We considered our modeling to represent a population-scale analysis; at this scale, spatial variation in habitat features should account for differences in elk use (Gaillard et al. 2010).

Defining Areas for Habitat-Use Modeling and Validation

We obtained elk locations from several studies, most spanning multiple years, conducted during 14 years in the Westside region (Fig. 17; Tables 1 and 7). We identified 13 independent capture efforts and associated telemetry data sets from these studies for use in model development and validation (Tables 1 and 7). All wild elk used in our analyses ($n=173$) were adult females captured and fitted with GPS or VHF collars, and locations were obtained systematically at intervals ranging from 20 min (GPS) to 1 week (VHF). Locations for GPS collars were recorded automatically at shorter intervals, whereas those for VHF collars were obtained via ground or aerial triangulation at least weekly. For GPS collars, location accuracy was high and precision was typical of such collars (<100 m; Hebblewhite and Haydon 2010, Tomkeiwicz et al. 2010); fix success (range: 93–98%; Table 7) and relocation frequency (15–20 min in all but the Pysht data set, which was every 4 hr) were also high. We limited our analyses to elk subjected to autumn hunting pressure, which represents most Westside elk populations, thus excluding telemetry studies for

non-hunted elk that resided entirely within national park boundaries or suburban areas. Prior studies have documented that responses of these elk to human disturbance would likely be different and affect predictions of habitat use (Thompson and Henderson 1998, Haggerty and Travis 2006, Stankowich 2008, Starr 2013).

From each data set, we selected elk locations recorded between 1 June and 31 August to define the summer modeling period (Wisdom et al. 2018a). We excluded telemetry data that overlapped hunting and rutting periods because elk movements and habitat use may change substantially during those times (Conner et al. 2001; Johnson et al. 2005; Storlie 2006; Proffitt et al. 2010, 2013). Thus, predictions of the habitat-use model do not extend beyond August, when several hunting seasons begin in western Oregon and Washington, including archery hunts for elk and rifle hunts for black-tailed deer. All animal handling was conducted following regulations set forth for implementing the Animal Welfare Act of 1966 and its subsequent amendments and adhered to standards adopted and published by the American Society of Mammalogists (Sikes et al. 2011).

We chose 5 of the GPS data sets for model development because of their superior quality, as noted previously. We used these telemetry data sets to delineate 5 areas for habitat-use modeling (modeling areas; Table 1). Although some GPS collars were programmed to collect locations frequently (e.g., every 15 or 20 min; White River 2004, 2005, 2007), we followed the advice of Kernohan et al. (2001) and assumed independence between locations to avoid constraining estimates of the local (population-level) seasonal ranges.

We defined perimeters of the 5 areas used for habitat model development based on 99% contours for fixed kernel density estimates (KDEs; Wand and Jones 1994) using Hawth's Analysis Tools (v3.27 ArcGIS extension, <http://www.spatialecology.com/htools>, accessed 5 Apr 2009) with smoothing parameter $h=1,000$ (default). Model development areas were located in 3 regions of Washington (Pysht, Green River, and White River; Table 1) and ranged in size from 7,135 ha (Pysht 2009) to 35,019 ha (White River 2007; Table 7; Appendix A). Some modeling areas overlapped modestly (Fig. 17), but each was defined by a unique year and capture effort. For example, the Muckleshoot Indian Tribe collared 13 elk in the White River drainage of western Washington in early 2004, and those collars were retrieved via animal capture in late 2004 (White River 2004; Table 7). An additional 6 collars were deployed on a new sample of elk in early 2005 (White River 2005). Then in 2007, another sample of 13 elk was captured and fitted with GPS collars within the same region (White River 2007).

We used the remaining 8 independent elk data sets for model validation and calculated MCPs to delineate model validation areas (Fig. 17; Table 1). These averaged 23,226 ha and ranged from just over 2,700 ha (Quileute 2006–2008) to 53,630 ha (Green-Cedar 2006–2009). We used MCPs rather than KDEs to define validation areas because data collection in these sites was most often with VHF collars, which provided fewer and less-precise locations. The MCPs were more robust to the smaller sample sizes of many of our validation data sets and included more available area compared to KDEs. Further, we anticipated that when biologists or managers used our models, they would

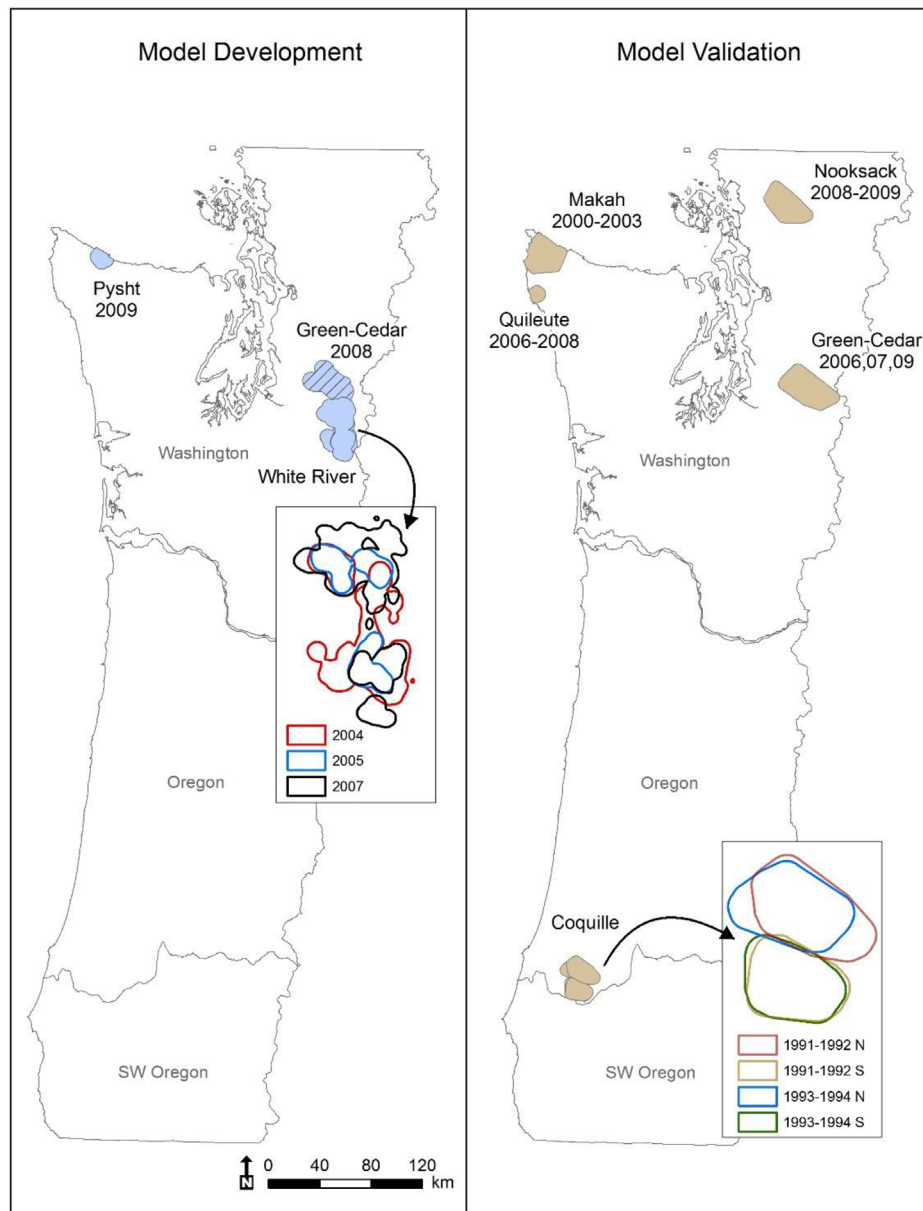


Figure 17. Western Oregon and Washington, USA (Westside region) and areas associated with telemetry data sets used for elk habitat-use model development (left) and validation (right).

seldom create kernels based on a representative sample of elk in the area but instead would identify project areas or larger regions. Collectively, these validation areas represented a diverse cross-section of environmental conditions in the Westside region (Appendix A).

Development of Habitat-Use Models

We adopted a hierarchical modeling approach by considering individual model development areas as replicates in generating a regional habitat-use model. This approach is analogous to that of treating individual animals as the primary sampling units when creating a population-level model for a single study site (e.g., Sawyer et al. 2006, Fieberg et al. 2010). We used a 4-step process to develop a regional elk habitat-use model by 1) measuring covariates at systematically selected circular sampling units within each habitat-use modeling area, 2) estimating the relative

frequency of use in the sampling units for all collared elk within each modeling area during summer, 3) modeling the relative frequency of use as the response variable in a generalized linear model (GLM) using a negative binomial (NegBin) habitat-use model, and 4) averaging coefficients across modeling areas to generalize habitat relationships and develop a regional model.

Following identification of population-level seasonal ranges for each data set, we took a systematic sample, based on a random starting location, of non-overlapping circular sampling units with 350-m radii from each modeling area (Sawyer et al. 2006, Nielson and Sawyer 2013). We then calculated the number of elk locations within each sampling unit (Fig. 18) along with values of covariates of interest (Appendix B). Center points of all sampling units were within a KDE, but portions of some circles may have fallen outside the 99% contours. These sampling units provided the response (number of elk locations) and covariates for

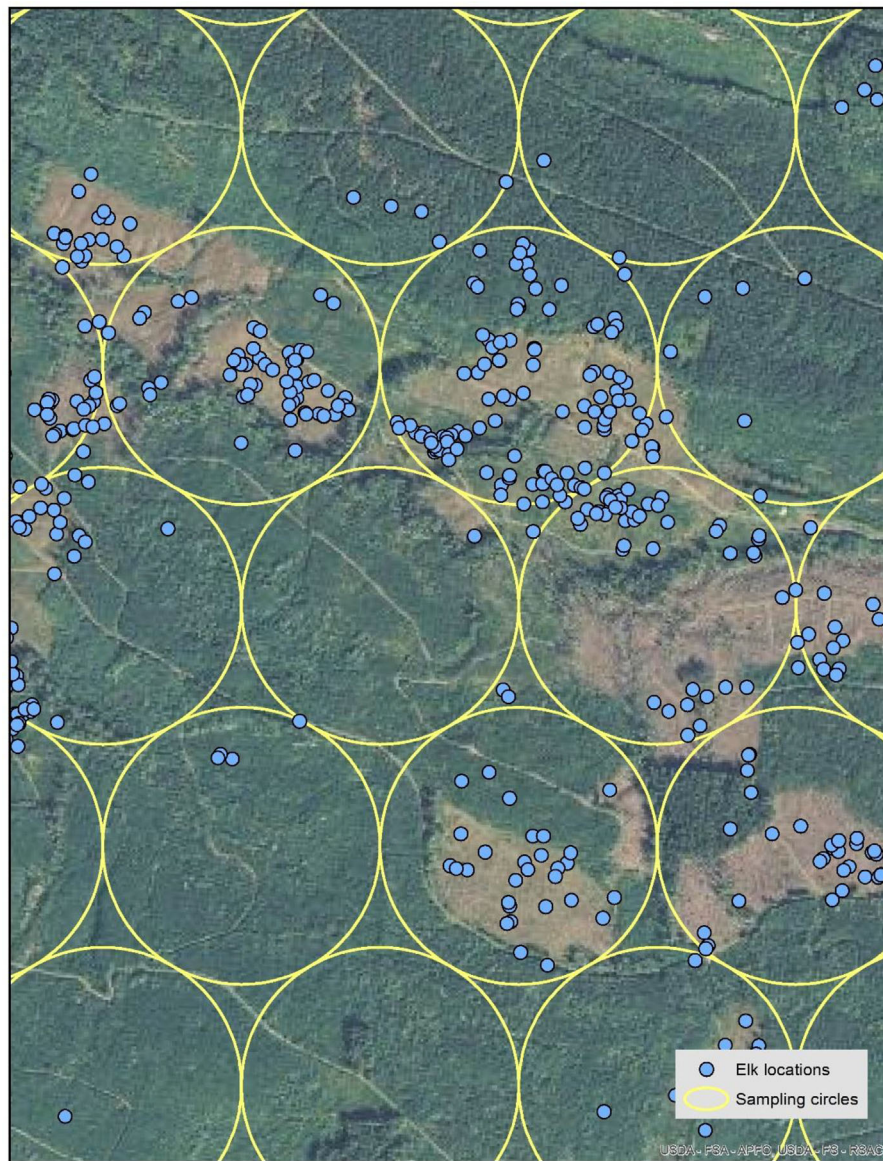


Figure 18. Example of a systematic sample of circular sampling units and elk telemetry locations.

estimating the habitat-use model. The number of sampling units for each modeling area ranged from 166 (Pysht 2009) to 805 (White River 2007). Nielson and Sawyer (2013) recommended choosing a sampling unit that is small enough to detect changes in animal movements while providing counts of locations that approximate a negative binomial distribution. During pre-analysis investigations, we considered sampling units of various sizes and determined that a 350-m radius circle was appropriate, largely based on the distribution of the number of GPS locations within the units, landscape heterogeneity, and mobility of sampled animals during summer. In addition, we ensured that the size of the sampling units exceeded the inherent error in GPS locations and in covariate layers considered during modeling (Nielson and Sawyer 2013).

We used a GLM to estimate the intensity of use for each modeling area as a function of covariates using the NegBin habitat-use model. This method is described by Nielson and Sawyer (2013) and is also found in Millsaugh et al. (2006) and

Sawyer et al. (2006, 2007, 2009). We considered a Bayesian hierarchical model estimated via Markov chain Monte Carlo methods, but the combined size of our data sets and the complexity of our model development process precluded use of this modeling approach because of its computational demand. We also attempted to fit a generalized linear mixed model with random effects for model development areas, but we experienced convergence issues even with the simplest models; thus we adopted a 2-stage approach to estimating a regional elk habitat-use model (Fieberg et al. 2010).

Potential for habitat-induced data loss (Frair et al. 2004, 2010; Nielson et al. 2009) was not a concern in modeling because of the high GPS fix success during the summer period (Table 7). All GPS fix schedules covered the 24-hour period during summer. We were not interested in creating a foraging-period model because our goal was to develop a more general habitat-use model that integrated multiple covariates, not just nutrition, to predict elk distributions. Moreover, we could not restrict our analysis to periods presumed to

capture foraging (e.g., crepuscular hours) because we would have been forced to discard all VHF data, which was largely diurnal (Table 7). Large numbers of locations recorded at regular intervals (e.g., 15–20 min), as was true for all but one of our GPS telemetry data sets, can result in counts of use within the circular sampling units that are quite large (hundreds or thousands). Although the NegBin is not influenced by temporal autocorrelation in animal locations, too many locations within some of the circular sampling units can result in counts of use that are not NegBin distributed (Nielson and Sawyer 2013). Thus, we elected to use at most the first location obtained every hour.

The NegBin involves regressing the number of animal locations within each circular sampling unit onto the covariates measured on those units. We applied the model in each individual modeling area; it was based on the commonly used NB2 formulation of this function (see below; Cameron and Trivedi 1998), which can be represented by

$$\ln[E(t_i)] \approx \ln(T) + \beta_0 + \beta_1 x_{1i} + \beta_2 x_{2i} \dots + \beta_p x_{pi} \quad (1)$$

where t_i is the number of GPS locations within sampling unit i , E represents the expected value, T represents the total number of GPS locations within the modeling area, β_0 is an intercept term, $\beta_1, \beta_2, \dots, \beta_p$ are coefficients to be estimated, and $x_{1i}, \dots, x_{pi}$ are the values of p covariates measured on sampling unit i . Inclusion of the offset term, $\ln(T)$, in Equation (1) simply scales the response to ensure modeling of relative frequency, or intensity of use (e.g., 0, 0.003, 0.0034, ...) instead of integer counts (e.g., 0, 1, 2, ...; Nielson and Sawyer 2013). We used the natural log of the number of locations obtained from a particular modeling area in summer as the offset term in Equation (1). The errors follow a negative binomial distribution.

Various NegBin model parameterizations exist, and distinctions are made based on the link function used and the assumed distribution of $\text{var}(Y)$. The NB2 (log link) is the most common parameterization (Cameron and Trivedi 1998), which specifies

that $\text{var}[Y] = u + u^2/\theta$ (Hilbe 2008). The term $\text{var}[Y]$ is the variance of the observed count of use (Y), u is the expected count of use, and θ is the dispersion parameter. The likelihood for the NB2 formulation can be found in Cameron and Trivedi (1998:71).

Covariate derivation and selection.—We developed an *a priori* list of potential landscape variables (covariates) by reviewing previously published elk habitat models (e.g., Wisdom et al. 1986, Edge et al. 1987, Roloff 1998, Sawyer et al. 2007). We initially considered >30 covariates (Appendix B, Table B1), but consultation with biologists and land managers helped us refine our list (Tables B2 and B4) by identifying factors believed to affect local elk populations and those most likely to be manageable (e.g., plant community attributes such as acceptable biomass or canopy cover) or easier to derive accurately and efficiently (e.g., roads open to the public vs. estimates of vehicle traffic).

We grouped covariates into 4 categories to predict elk habitat use: 1) nutrition, 2) human disturbance, 3) vegetation, and 4) physical (Fig. 19). Our initial process of covariate selection and reduction resulted in 6 nutrition covariates, 10 human disturbance covariates, 11 vegetation covariates, and 13 physical covariates for evaluation (Appendix B, Table B1). Nutrition covariates reflected potential energy accrual, whereas human disturbance covariates generally reflected energy costs, such as flight responses to motorized traffic. Vegetation covariates may correspond to either energy gain or loss (for example, higher quality and abundance of forage in open-canopy forests versus energy costs incurred in traveling to distant cover patches). Likewise, physical covariates may relate to energy balance, such as increased energetic costs when traveling on steep slopes (Kie et al. 2005) versus thermal benefits of north aspects in summer (Ager et al. 2003). Although physical covariates like aspect cannot be managed directly, we retained this group because these features have been consistent predictors of habitat use by elk in prior studies (Johnson et al. 2000, Ager et al. 2003, Sawyer et al. 2007,

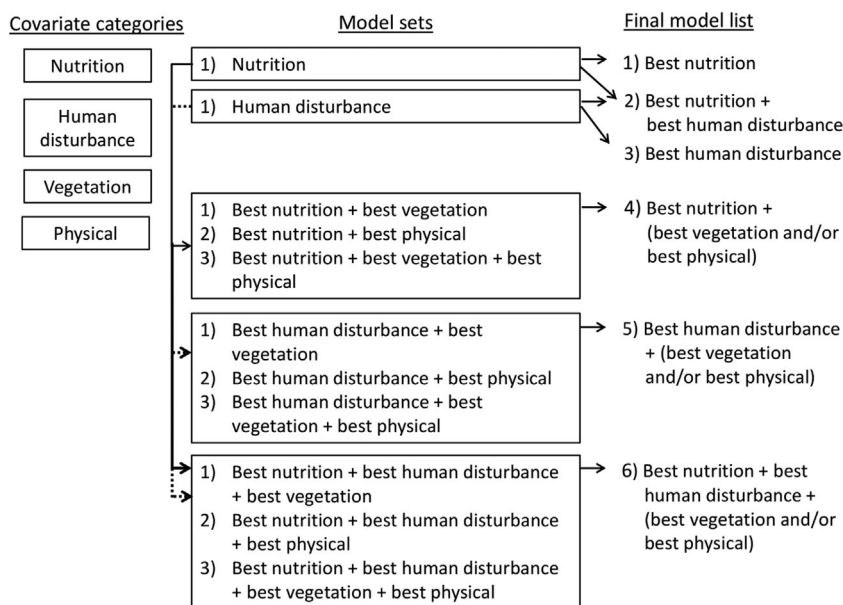


Figure 19. Description of the process used to develop the habitat-use model for elk in western Oregon and western Washington, USA.

Barbknecht et al. 2011, Coe et al. 2011, Harju et al. 2011) and provide context for model predictions. We also modified some covariates, such as canopy cover, when required to match the vintage of associated elk telemetry data. When telemetry locations spanned multiple years for a single data set, we selected covariate values from the year in which most elk locations were obtained (Appendix B).

We calculated covariate values within each cell on a 30-m $\times$ 30-m grid encompassing our modeling areas, using either the average (e.g., mean slope), percent coverage (e.g., percent canopy cover), or distance from the center point of each 350-m radius sampling unit (e.g., distance to nearest forage patch). Distance to nearest road open to public motorized use (distance to open road) was based on grids extending 4 km beyond the modeling area boundaries. Our intent was to account for elk reacting to roads close to, but outside, the defined modeling area. The 4-km buffer for distance to open road was based on earlier studies (e.g., Rowland et al. 2000, Sawyer et al. 2007) and preliminary analyses suggesting elk did not respond to roads beyond 4 km. Thus, if distance to nearest open road was >4 km, distance was truncated at 4 km for analysis. Similarly, the distance to nearest cover-forage edge covariate (distance to edge; Appendix B) accounted for edges outside the modeling area but within 4 km of the boundary. Before analysis, we removed circular sampling units centered on or encompassing >38.5 ha (50% of the circle) of a land cover type considered non-habitat, such as rock, water, ice, or development-urban (Appendix B, Table B3).

We derived some covariate layers in a GIS with >1 data source, which allowed us to compare sources (e.g., X_a and X_b) and qualitatively evaluate their accuracy. If we thought a data source had potential for large errors, or errors appeared small but inconsistent on a regional scale, we dropped the covariate derived from that source. To further screen covariates, we used histograms to identify substantial differences in distributions of covariates between data sets or across the larger regional landscape. These differences could indicate potential problems in either identifying a common relationship between elk habitat use and that covariate, or applying our final elk habitat-use model(s) to the region. With large differences in distributions, we would err by predicting elk habitat use outside the range of the data used for model estimation (Neter et al. 1996). Thus, if we identified a marked difference in distributions across data sets, we dropped the covariate.

We used a pairwise correlation analysis to further reduce the number of covariates in each category prior to modeling, which diminished the potential for deleterious effects of collinearity on model estimates. If ≥ 2 covariates had a Pearson's correlation coefficient of $|R| > 0.6$, we took 1 of the following approaches to reduce chances of collinearity destabilizing the NegBin model: 1) we dropped 1 of the 2 correlated covariates; 2) we did not allow both covariates to enter the same model together; or 3) we carefully monitored model estimates to ensure that model stability was not compromised. If 2 or more covariates were highly correlated, and 1 was clearly easier to derive and interpret and had more relevance to management, we retained only that covariate and dropped the other(s) prior to modeling. However, if this choice was unclear and the correlated covariates were in the same category (e.g., nutrition, physical), we allowed only 1 of the covariates to enter the model based on support in the data

according to Akaike's Information Criterion (AIC; Burnham and Anderson 2002). Although a pairwise correlation analysis prior to modeling is useful for identifying potential multicollinearity issues, smaller pairwise correlations can affect model estimates, and the method cannot identify scenarios where the linear combination of 2 or more model covariates is correlated to another covariate. Major changes in estimates of coefficients (e.g., negative to positive) and likelihood-based estimates of standard errors (small to large) provide direct evidence of multicollinearity issues. Thus, we carefully monitored estimates of coefficients and standard errors during the model building procedure to ensure that multicollinearity was not influencing model estimates.

Model selection.—With our refined set of covariates, we fit a univariate model for each covariate within a covariate category, such as physical, to data from each habitat modeling area. We discarded covariates if AIC results revealed inconsistent coefficients across study areas or confidence intervals spanned 0. We then ranked the remaining models by AIC values. A rank of 1 indicated the model had the lowest AIC score in the category. Finally, we summed ranks of models within each category across modeling areas to identify the consistently best model for that category (lowest AIC rank). For example, consider a covariate category with 3 univariate models, for which AIC ranks indicate that model 1 has a rank of 1 in 3 of the 5 habitat-use modeling areas and ranks of 2 and 3 in the 2 remaining areas. Thus, model 1 has a sum of ranks = 8 ($3 \times 1 + 2 + 3$). If models 2 and 3 have summed ranks of 10 and 12, respectively, then model 1 has the most support from the data. Using this approach, rather than the sum of likelihoods or AIC values, gives equal weight to each data set in identifying the best models. The ranks also highlight differences and similarities across modeling areas.

We used a 2-stage information-theoretic approach (Burnham and Anderson 2002, DeVore et al. 2016) in model development. This approach allowed us to avoid evaluating all possible combinations of covariates as competing models without regard to their ecological meaning or intended uses, and ensured that we primarily considered mechanistic covariates relevant to management. First, we identified sets of candidate models that combined covariates from different categories (Fig. 19). Then, we fit each model within a model set to telemetry data from each habitat modeling area (Table 7) and ranked the models by AIC values, as described previously for covariate selection. The lowest of the summed ranks of individual models within each model set across modeling areas identified the consistently best model.

Following identification of the top model within each set, we created a final model set by combining the competitive models from each set representing the best nutrition, human disturbance, vegetation, and physical models. This process resembled that of Beck et al. (2006) in developing habitat models for elk based on alternative explanations of factors influencing selection such as forage and distance to roads versus forage and topography. We required that each model in the final list contain either the best nutrition or best human disturbance model. This decision was based on our confidence that nutrition and human disturbance had stronger mechanistic support than other covariate groups (vegetation and physical). These covariates have clearly demonstrated relationships to ecological processes of energy

Table 7. Telemetry data used to develop and validate elk habitat-use models in western Oregon and Washington, USA.

Model use	Data set (study area and year)	Technology ^a	Number of animals	Number of locations	Fix success ^b	Data source
Development	Green-Cedar 2008	GPS	17	26,480	94	Muckleshoot Indian Tribe
	Pysht 2009	GPS	6	3,228	97	Lower Elwha Klallam Tribe
	White River 2004	GPS	13	28,355	93	Muckleshoot Indian Tribe
	White River 2005	GPS	6	11,923	97	Muckleshoot Indian Tribe
	White River 2007	GPS	13	28,692	98	Muckleshoot Indian Tribe
Validation	Coquille North 1991–1992	VHF	16	316		Oregon State University
	Coquille North 1993–1994	VHF	20	180		Oregon State University
	Coquille South 1991–1992	VHF	13	225		Oregon State University
	Coquille South 1993–1994	VHF	15	113		Oregon State University
	Green-Cedar 2006, 2007, 2009	GPS	23	69,150	96	Muckleshoot Indian Tribe
	Makah 2000–2003	VHF	21	820		Makah Indian Tribe
	Nooksack 2008–2009	GPS	7	3,618	88	Nooksack Indian Tribe
	Quileute 2006–2008	GPS	3	14,686	94	Quileute Tribe

^a Global positioning system (GPS) or very high frequency radio telemetry (VHF).

^b Mean fix success of GPS collars, reported as percentage of attempted locations for which a successful location was obtained. Not applicable for VHF collars.

acquisition (nutrition) or energy loss (human disturbance) and can be manipulated by managers to change habitat use by elk. There is less empirical evidence of underlying mechanisms for patterns of elk use in relation to vegetation covariates. Moreover, some vegetation covariates were predictors in the nutrition model (e.g., overstory canopy cover), and thus would have been redundant in habitat-use modeling. Our model development process used the AIC ranking procedure described above. In summary, we first identified the best model in each of the 4 covariate categories, and then identified the best models using combinations of these 4 models, culminating in a final list of models from steps 1–4 (Fig. 19).

From the final list of 6 models (Fig. 19), we identified the top-ranked model for each model development area using AIC. We then summed AIC ranks across areas to identify a final habitat-use model for the region. We estimated this regional model (hereafter referred to as the Westside habitat-use model) by averaging coefficients from the final model across the 5 modeling areas. This 2-stage approach (Millspaugh et al. 2006, Fieberg et al. 2010) allowed us to investigate differences in elk habitat use among studies during model development yet synthesize results through meta-analysis of disparate data sets into 1 final regional model for distribution to managers. Although each study-area model represents a measure of probability of use, the regional model based on the average of coefficients from individual modeling areas represents the relative probability of use because predictions from the regional-level model reflect geometric means of study-area probabilities rather than true probabilities (Nielson and Sawyer 2013).

To estimate 90% CIs for coefficients in the Westside habitat-use model, we bootstrapped (Manly 2006) the primary sampling units—individual elk habitat modeling areas—1,000 times and re-estimated regional model coefficients for each sample. We used the central 90% of the 1,000 estimates for each coefficient as the CI (percentile method). We used a similar approach to calculate 90% CIs for coefficients of the 5 individual modeling areas, except the primary sampling units at that level were the collared elk. We followed the premise of Adams et al. (1997), who concluded that bootstrapping methods are more conservative than standard confidence limits for meta-analysis of ecological data.

We evaluated the final model for goodness of fit using the sum of the deviance residuals in a chi-square test (Hilbe 2008). A *P*-value < 0.1 from the chi-square test would indicate lack of fit

and the potential that the data were not distributed as a NegBin. We also investigated whether spatial correlation existed in model residuals among the circular sampling units within each model development area using Moran's *I* (Moran 1950). A high Moran's *I* value would indicate a violation of independence in the residuals and model assumptions.

Model Interpretation

To aid in model interpretation, we calculated use ratios and marginal plots for coefficients in the Westside habitat-use model. We computed use ratios, similar to selection ratios (McDonald et al. 2006), from the estimated coefficient for each covariate using $\left[\exp(\hat{\beta}_j) - 1 \right] \times 100\%$, which identifies the change in percentage increase or decrease in the predicted probability of use with a 1-unit increase in the covariate X_j , holding all other variables constant. Although it is unrealistic to expect the value of 1 covariate to change while others remain constant, use ratios are useful for evaluating the marginal contribution of individual covariates. Similarly, we used marginal plots to visualize how predictions of elk use changed across the range of observed values for a single covariate while values of other covariates remained constant.

In addition to producing marginal plots, we calculated standardized partial regression coefficients (Zar 2010) for all variables in the Westside habitat-use model. The absolute values of standardized coefficients can indicate the relative importance of covariates in predicting use by elk (Millspaugh et al. 2006, Zar 2010). However, strict interpretation requires the covariates to be independent, which is usually not true. Thus, we used a combination of use ratios, marginal plots, standardized coefficients, and CIs for the final model to help identify and understand the relative importance of each covariate in the habitat-use model.

We mapped predictions of the Westside habitat-use model on a 30-m × 30-m grid that covered each modeling area, excluding cells identified as non-habitat (Appendix B). We then assigned the model prediction for each grid cell a value of 1 to 4 based on the quartiles of the distribution of predictions for each modeling area and classified areas as low use (first quartile), medium-low use (second quartile), medium-high use (third quartile), or high use (fourth quartile); each quartile represented 25% of the specific modeling area. We also mapped covariates of the Westside

habitat-use model within each modeling area to display the range of values in each area and aid in interpretation of observed spatial patterns of predicted elk use.

Model Validation

We evaluated performance of the regional model with 8 independent data sets using locations of female elk not used during covariate selection and model estimation (Table 1). Many of these locations were recorded with VHF radiotelemetry (Table 7) and thus were limited in number and to daylight or crepuscular hours only. For validation data collected via GPS (Table 7), fix success averaged >84% for data collected at Nooksack, >93% for Quileute, and >90% for Green-Cedar. For each validation data set, we mapped predictions of the regional model on a 30-m $\times$ 30-m grid that covered an MCP developed using all elk locations collected in that area between 1 June and 31 August. We categorized elk locations from Coquille as separate north and south data sets for 1991–1992 and for 1993–1994 because of the original sampling scheme of this study (Cole et al. 1997), and used all recorded locations from the 4 data sets to create MCPs (Table 1; Appendix A).

We assigned each cell of the grid to 1 of 20 equal area-sized prediction bins using percentiles of the distribution of predictions for that grid. Thus, prediction bin 1 had the lowest 5% of predicted values on the grid, and bin 20 had the highest 5%. We calculated a Spearman rank correlation (r_s) between bin rank and the number of elk locations that occurred in each of the 20 bins (Boyce et al. 2002, Sawyer et al. 2009). We performed all statistical analysis in the R language and environment for statistical computing (R version 2.11.1, www.r-project.org, accessed 6 May 2010). We estimated the NegBin using the glm.nb function and the NB2 formulation available in the MASS contributed package (Venables and Ripley 2002).

RESULTS

Covariate Selection and Model Development

Following model selection in AIC and removal of candidate models with inconsistent or nonsignificant coefficients across study areas, we ultimately retained 4 covariates from the nutrition category for model development: mean DDE, mean accepted biomass (AB), mean of pixels with DDE ≥ 2.4 (marginal, good, or excellent [MGE]; Cook et al. 2004, 2018), and percentage of the circular sampling unit with DDE values ≥ 2.4 (% MGE; Appendix B, Tables B1 and B2). For human disturbance, we brought forward only 1 covariate, distance to open road. For the vegetation and physical covariate categories, only 1 covariate remained in each after pre-analysis screening and model selection: distance to edge (vegetation category) and mean slope (slope; physical category; Appendix B, Table B2).

We developed 3 models from the 4 covariates in the nutrition model set; 2 were univariate (DDE, AB), and the third combined 2 covariates (MGE and % MGE) with an interaction term (Table 8). Three of the nutrition covariates (DDE, AB, and MGE) were highly correlated and thus could not be included in the same model. We created the third model in this set to combine aspects of diet quality (MGE) and forage quantity (% MGE), predicting that elk seek patches that offer high levels of DDE. The best nutrition model, DDE, had a summed rank of 8 and was the top performer in 3 of 5 modeling areas (Table 8). The AIC weights (i.e., model strength of evidence) for the DDE model ranged from 0.005 to 0.534 among modeling areas (Appendix D, available online in Supporting Information).

We created 2 human disturbance models with the distance to open road covariate: a univariate model and one with both linear and quadratic terms. Exploratory analysis of elk locations in relation to roads revealed that elk use did not consistently increase linearly

Table 8. Ranks of models to predict habitat use by elk in summer in western Oregon and Washington, USA, within each of 5 model development areas. Models are organized by model set and listed in order within each set from best to worst as indicated by the sum of ranks (lower sum is better) for each model across areas.

Model set	Model	Model development area ^a					Summed rank
		GC08	PY09	WR04	WR05	WR07	
Nutrition	DDE ^b	1	1	2	1	3	8
	AB ^c	2	2	3	2	1	10
	MGE ^d , %MGE, MGE $\times$ %MGE	3	3	1	3	2	12
Human disturbance	Distance to open road	1	1	2	2	1	7
	(Distance to open road) ²	2	2	1	1	2	8
Nutrition + (vegetation and/or physical)	DDE, distance to cover-forage edge, slope	1	2	1	2	1	7
	DDE, slope	2	1	2	1	2	8
	DDE, distance to cover-forage edge	3	3	3	3	3	15
Human disturbance + (vegetation and/or physical)	Distance to open road, distance to cover-forage edge, slope	1	2	1	1	1	6
	Distance to open road, slope	2	1	3	2	2	10
	Distance to open road, distance to cover-forage edge	3	3	2	3	3	14
Nutrition + human disturbance + (vegetation and/or physical)	DDE, distance to open road, distance to cover-forage edge, slope	1	2	1	2	1	7
	DDE, distance to open road, slope	2	1	2	1	2	8
	DDE, distance to open road, distance to cover-forage edge	3	3	3	3	3	15

^a Codes indicate model development area and year: GC08 = Green-Cedar 2008; PY09 = Pysht 2009; WR04 = White River 2004; WR05 = White River 2005; WR07 = White River 2007.

^b Dietary digestible energy (kcal/g) within a circular sampling unit.

^c Accepted biomass (kg/ha; biomass of plants that elk neither significantly avoided nor selected and those that elk significantly selected).

^d Marginal, good, or excellent categories of DDE; values ≥ 2.4 kcal/g.

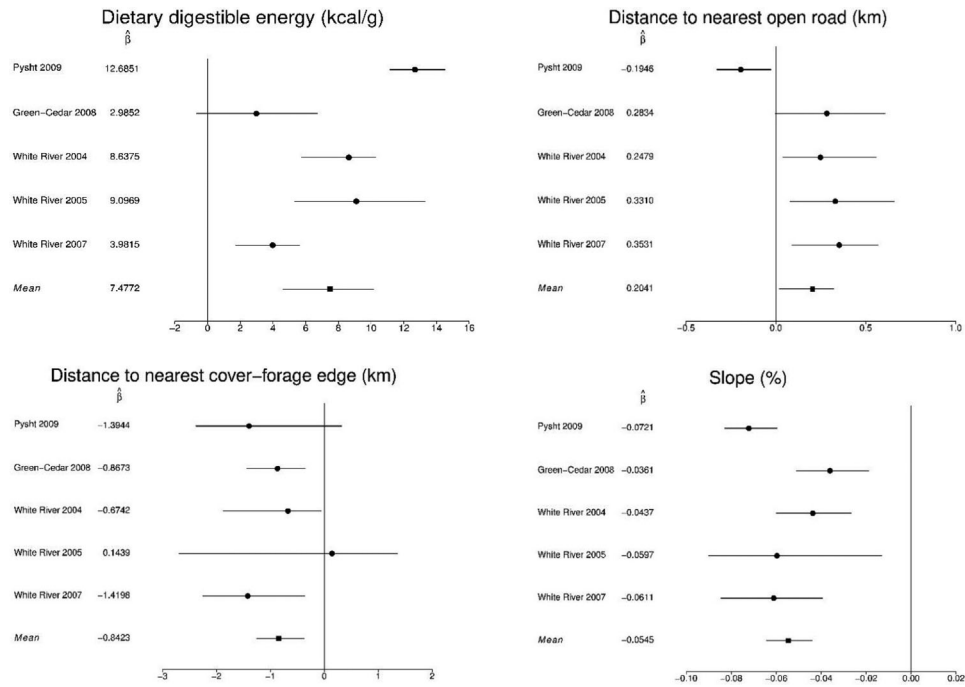


Figure 20. Coefficients ($\hat{\beta}$) and 90% confidence intervals for the 4 covariates in the best elk habitat-use model estimated for each of 5 model development areas and averaged across areas, western Oregon and Washington, USA.

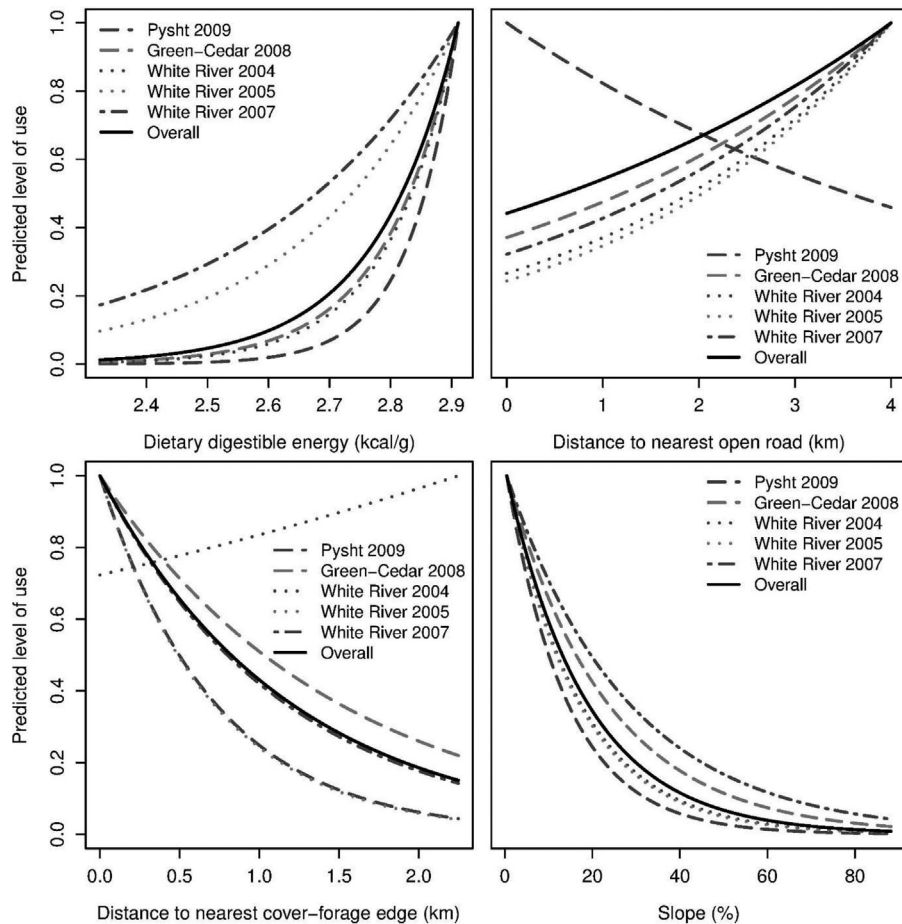


Figure 21. Marginal plots of the 4 covariates in the best elk habitat-use model estimated for each of 5 model development areas and averaged across areas, western Oregon and Washington, USA.

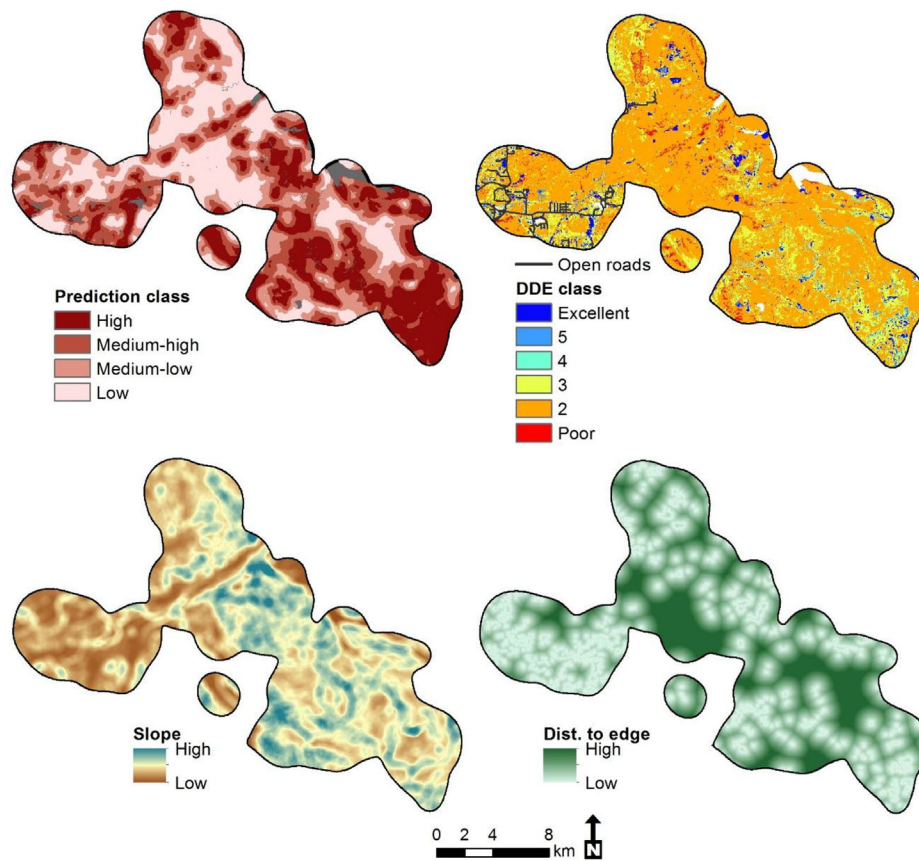


Figure 22. Predicted habitat use by elk, classified into 4 equal-area bins (i.e., each representing 25% of the modeling area) for the Green-Cedar 2008 model development area in western Washington, USA, based on the regional Westside model. Values for model covariates are also displayed, including dietary digestible energy (DDE), mean slope (%), and distance to nearest cover-forage edge (dist. to edge; km). Roads open to public motorized use are displayed on the DDE map. Masked areas represent non-habitat (e.g., rock, water) and are displayed in gray in the predicted use map and white in the DDE map.

among modeling areas as distance to open road increased. However, the best model, distance to open road, ranked first in 3 of the 5 modeling areas (summed rank = 7; Table 8). In these 3 sites AIC weights were relatively high (>0.63), indicating strong support for this model in contrast to the quadratic form (Appendix D).

We next combined distance to edge and slope with the best nutrition and human disturbance models to create new model sets (Fig. 19). For the nutrition + (vegetation and/or physical) model set, we evaluated 3 models that contained DDE and either slope or distance to edge or both; the best model contained all 3 covariates (Table 8). This model ranked first in 3 of 5 modeling areas (summed rank = 7), and AIC weights ranging from 0.271 to 0.972 indicated uniformly strong support, especially in the Green-Cedar 2008 and White River 2004 data sets (Appendix D). We then compared 3 models in the human disturbance + (vegetation and/or physical) model set. Similar to results for the previous model set, the best model in this group contained all 3 covariates: distance to open road, distance to edge, and slope (Table 8). The summed rank of 6 for this model indicated that it was the best performer for all but 1 data set (Pysht 2009), where it ranked second behind distance to open road and slope.

We then combined the best nutrition, human disturbance, vegetation, and physical models in another model set, with the constraint that each model contained nutrition and human

disturbance covariates. The best model included all possible covariates (i.e., DDE, distance to open road, distance to edge, and slope; Table 8). This model ranked first in 3 areas and second in the remaining 2; AIC weights ranged from 0.277 to 0.990 (Appendix D).

We evaluated one additional candidate model, combining the best nutrition and human disturbance models (i.e., DDE and distance to open road) with the best performers from the 5 model sets described above (Fig. 19). The best model in the final set ranked first in every habitat-use modeling area (summed rank = 5) and included 4 covariates: DDE, distance to open road, distance to edge, and slope (Table 9). The AIC weights for this model ranged from 0.553 (PY09) and 0.750 (GC08) to >0.890 in the 3 remaining modeling areas, indicating consistent, and strong regional support (Appendix D). The second-best model had a summed rank of 12 and was similar to the best model but lacked the distance to open road covariate (Table 9). Two covariates, distance to edge and slope, occurred in each of the 3 best models (Table 9). Distance to open road was the model least supported by the data in our final list; the summed rank was 35 and all AIC weights approached zero (Appendix D).

We created the Westside habitat-use model by averaging estimated coefficients for each covariate in the final model across the 5 model development areas (Table 1). Predicted use ($\hat{w}$) from the Westside habitat-use model was:

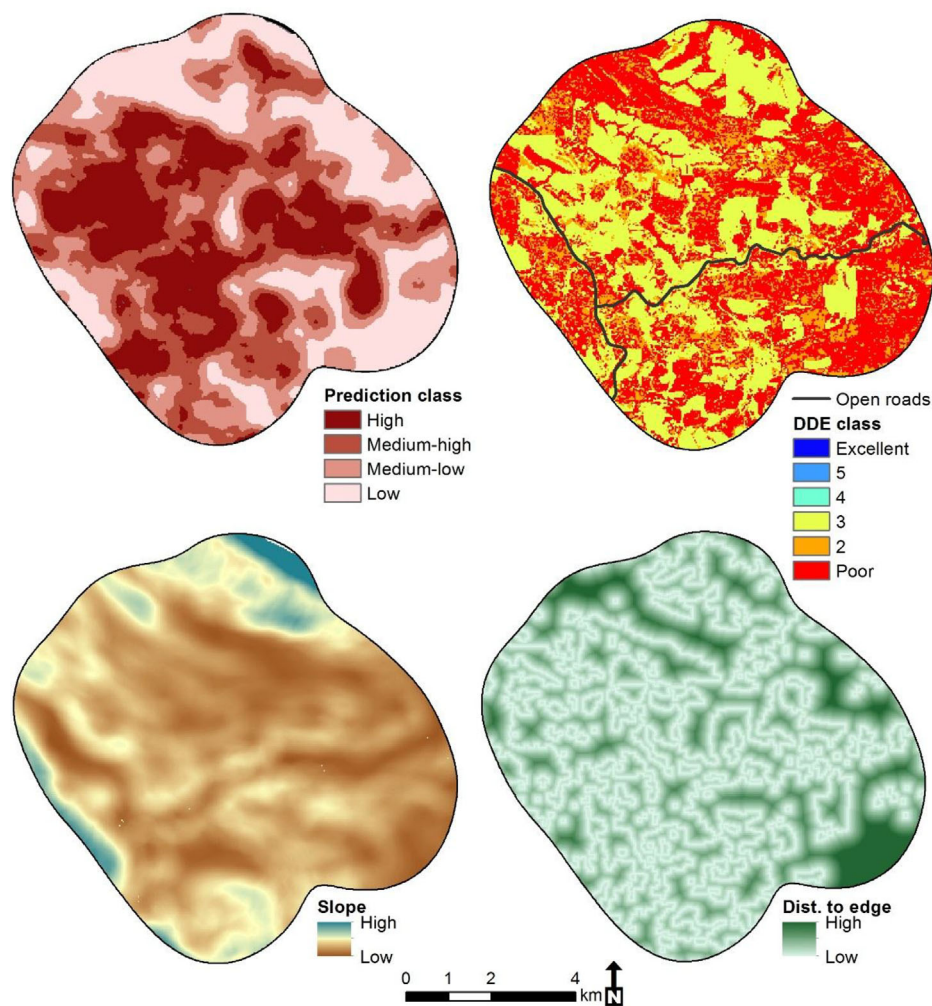


Figure 23. Predicted habitat use by elk, classified into 4 equal-area bins (i.e., each representing 25% of the modeling area) for the Pysht 2009 model development area in western Washington, USA, based on the regional Westside model. Values for model covariates are also displayed, including dietary digestible energy (DDE), mean slope (%), and distance to nearest cover-forage edge (dist. to edge; km). Roads open to public motorized use are displayed on the DDE map.

$$\hat{w} = \exp(-24.2389 + [7.4772 \times \text{DDE}] + [0.2041 \times \text{distance to open road}] - [0.8423 \times \text{distance to edge}] - [0.0545 \times \text{slope}])$$

Goodness-of-fit tests for each study area resulted in P values between 0.20 (White River 2005) and 0.84 (Pysht). There was no evidence of lack of fit (i.e., that the data did not fit a negative binomial distribution), and spatial correlation in the residuals for the circular sampling units was extremely low in each study area. All Moran's I values for distances equal to 700 m (nearest neighbors) ranged from 0.07 to 0.21. Spatial correlation declined to near 0 within 2,100 m.

Model Interpretation

Coefficients for the final habitat-use model indicated that elk were most likely to occupy sites with greater DDE, far from roads open to the public, close to cover-forage edges, and with relatively gentle slopes (Table 10). Coefficients were generally consistent among modeling areas, with some exceptions

(Fig. 20). For example the estimated coefficient for distance to edge in White River 2005 was positive, but the 90% CI included 0; thus the relationship was not statistically significant at an alpha level of $\alpha = 0.10$. The estimate for DDE in Green-Cedar 2008 was also not statistically significant (Fig. 20). Moreover, there was a negative and statistically significant ($\alpha = 0.10$) relationship between elk habitat use and distance to open road in Pysht (2009). None of the CIs for the averaged coefficients for the 4 predictor covariates included 0, however, indicating that we identified elk habitat-use relationships that were consistent and robust among data sources (Fig. 20). Based on standardized coefficients, changes in slope (-0.949) were relatively most important in predicting habitat use, followed by DDE (0.656), distance to edge (-0.305), and distance to open road (0.300). Use ratios for the Westside habitat-use model indicated an increase in relative probability of use by elk with increases in DDE and distance from open roads, but decreases in relative probability of use with increasing distance to edge and slope (Table 10).

Predicted probability of use by elk, as demonstrated by marginal plots, increased steadily with increasing DDE across all 5

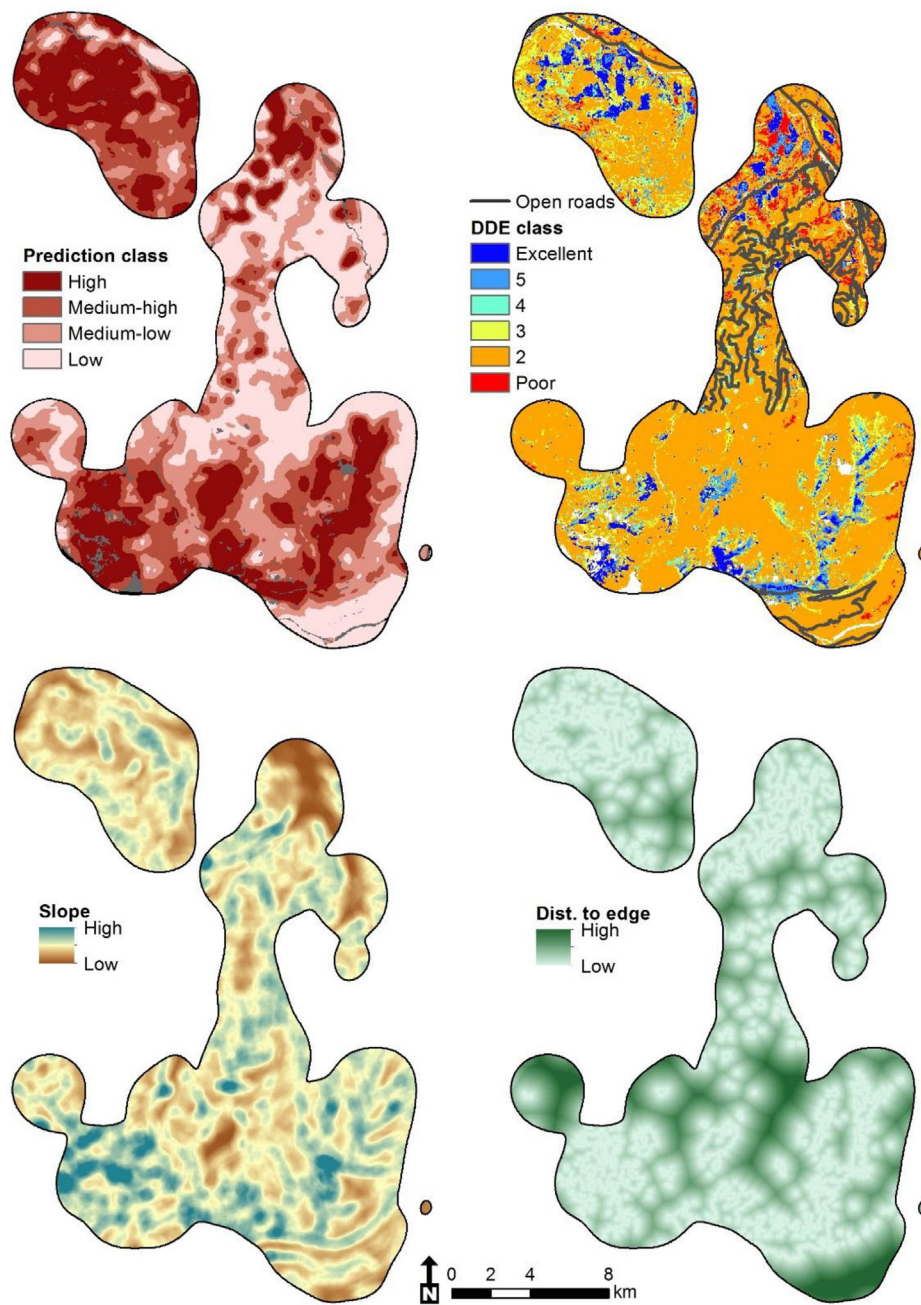


Figure 24. Predicted habitat use by elk, classified into 4 equal-area bins (i.e., each representing 25% of the modeling area) for the White River 2004 model development area in western Washington, USA, based on the regional Westside model. Values for model covariates are also displayed, including dietary digestible energy (DDE), mean slope (%), and distance to nearest cover-forage edge (dist. to edge; km). Roads open to public motorized use are displayed on the DDE map. Masked areas represent non-habitat (e.g., rock, water) and are displayed in gray in the predicted use map and white in the DDE map.

modeling areas, with the curvilinear response rising markedly at DDE levels exceeding 2.7 (Fig. 21). Predicted use also increased with increasing distance from roads in all areas, with the exception of Pysht 2009. Elk use was predicted to decline with increasing distance to edge, with the exception of White River (2007). Last, predicted use decreased sharply in all areas as slope increased between 0 and 40%.

Patterns of predicted use mapped in each model development area revealed high variability and patchiness of use as a result of the distribution and interaction of model covariates in each site (Figs. 22–26). For example, in Pysht (2009), where only 2

highways transected the site and nutrition was the most depauperate among modeling areas, predicted use was strongly aligned with nutrition but not roads (Fig. 23). Areas of steep slopes that were far from edges also showed low predicted use (Fig. 23). By contrast, in White River 2007, bands of low levels of predicted use closely aligned with open roads, especially in the southeastern edges of the area (Fig. 26). In Green-Cedar 2008 (Fig. 22), nutrition was uniformly low (predominantly low-marginal; Table 2) and not closely aligned with patterns of habitat use other than in the southeastern lobe of the kernel, where pockets of higher DDE values co-occurred with the

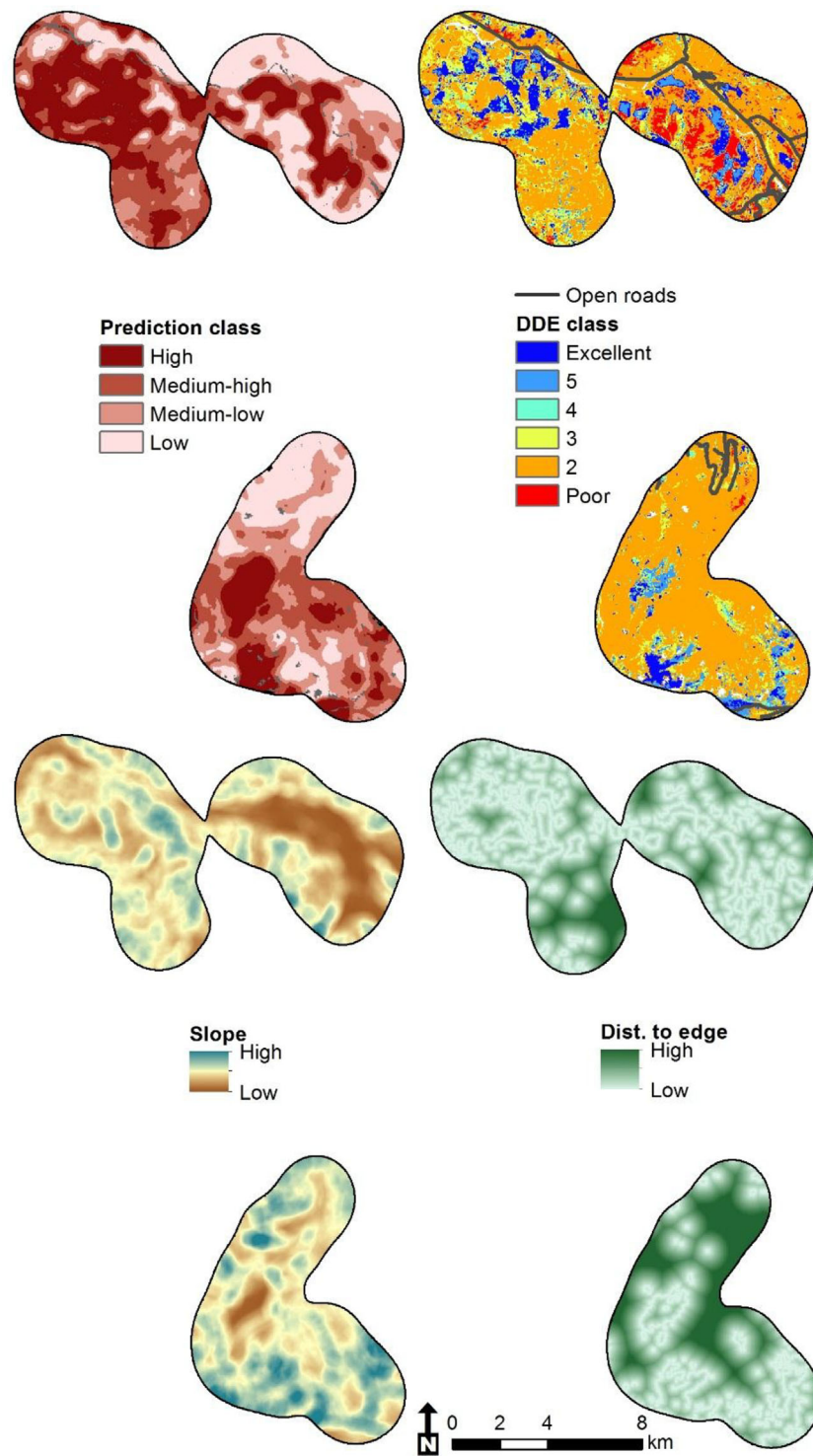


Figure 25. Predicted habitat use by elk, classified into 4 equal-area bins (i.e., each representing 25% of the modeling area) for the White River 2005 model development area in western Washington, USA, based on the regional Westside model. Values for model covariates are also displayed, including dietary digestible energy (DDE), mean slope (%), and distance to nearest cover-forage edge (dist. to edge; km). Roads open to public motorized use are displayed on the DDE map. Masked areas represent non-habitat (e.g., rock, water) and are displayed in gray in the predicted use map and white in the DDE map.

absence of open roads. By contrast, the western lobe had similarly good patches of DDE and several open roads that likely had low traffic rates, but these roads led to several small subdivisions that were masked from our analysis but may have influenced use by elk.

Model Validation

Spearman rank correlation coefficients between predicted and observed use for the final Westside habitat-use model ranged from 0.32 in Coquille North 1993–1994 to 0.99 in Green-Cedar (2006, 2007, 2009; Table 11). The mean correlation coefficient across

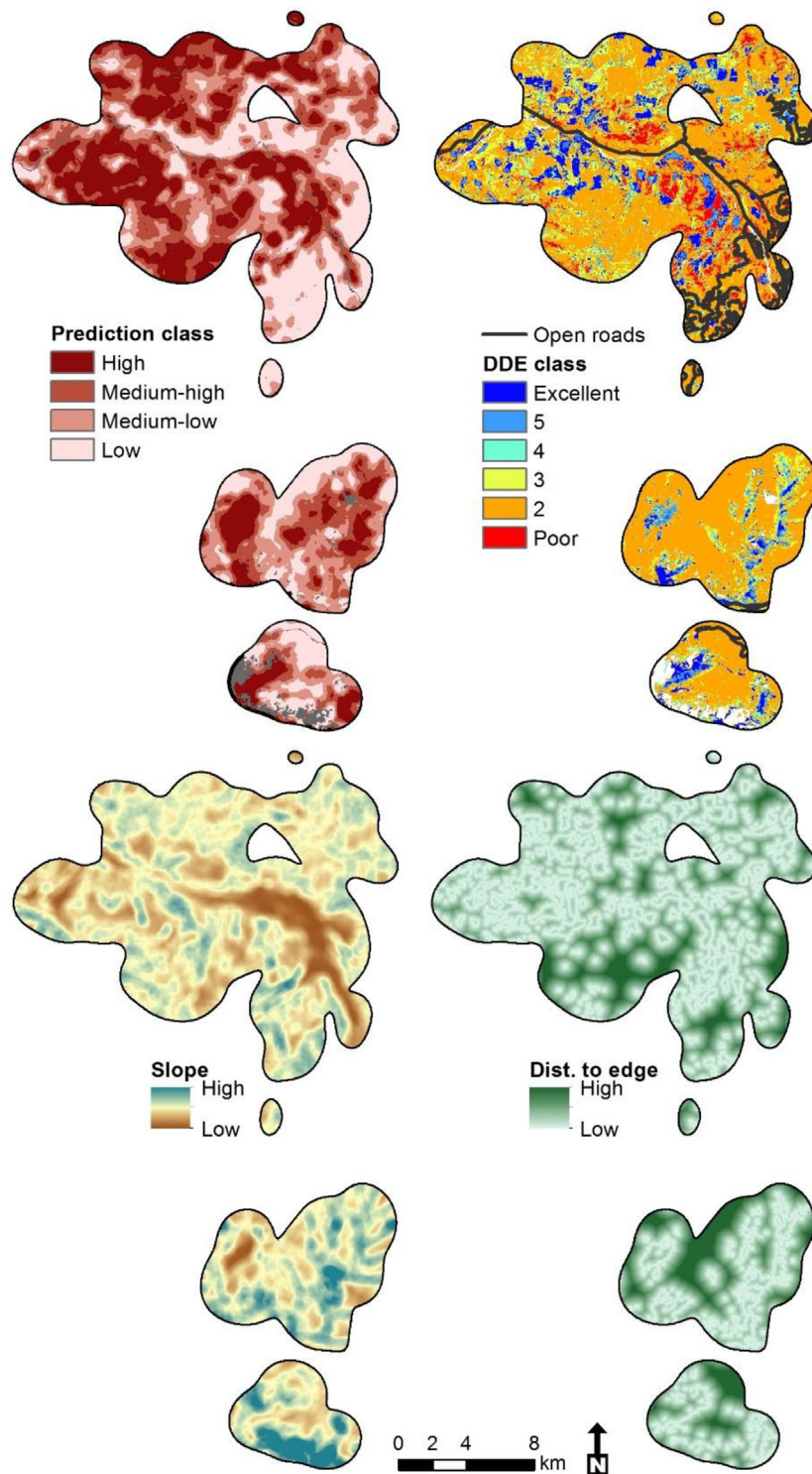


Figure 26. Predicted habitat use by elk, classified into 4 equal-area bins (i.e., each representing 25% of the modeling area) for the White River 2007 model development area in western Washington, USA, based on the regional Westside model. Values for model covariates are also displayed, including dietary digestible energy (DDE), mean slope (%), and distance to nearest cover-forage edge (dist. to edge; km). Roads open to public motorized use are displayed on the DDE map. Masked areas represent non-habitat (e.g., rock, water) and are displayed in gray in the predicted use map and white in the DDE map.

validation areas was 0.77 (90% CI = 0.63–0.90). Correlations were higher in the 4 validation sites in Washington ($r_s \geq 0.96$) than in the 4 in Oregon ($r_s = 0.32$ –0.87). Elk telemetry locations were generally clustered within higher prediction classes, with few observations of elk in the lowest-ranked classes (Appendix E, available online in Supporting Information).

DISCUSSION

Our hypothesis that habitat use by elk in western Oregon and Washington would be driven by a suite of covariates related to energy balance was well supported; our final model included 1) a direct measure of energy acquisition (DDE); 2) a metric of

Table 9. Ranks of the final set of candidate models used to predict habitat use by elk in summer within 5 model development areas in western Oregon and Washington, USA. Models are listed in order from best to worst as indicated by summed ranks; a summed rank of 5 would indicate that a model was the best performer in all 5 areas.

Model number	Model	Model development area ^a					Summed rank
		GC08	PY09	WR04	WR05	WR07	
6	DDE ^b , distance to open road, distance to cover-forage edge, slope	1	1	1	1	1	5
4	DDE, distance to cover-forage edge, slope	3	2	2	2	3	12
5	Distance to open road, slope, distance to cover-forage edge	2	6	3	3	2	16
1	DDE	5	5	5	4	5	24
3	DDE, distance to open road	6	3	4	5	6	24
2	Distance to open road	7	7	7	7	7	35

^a Codes indicate model development area and year: GC08 = Green-Cedar 2008; PY09 = Pysht 2009; WR04 = White River 2004; WR05 = White River 2005; WR07 = White River 2007.

^b Dietary digestible energy (kcal/g) within a circular sampling unit.

human disturbance and thus potential energy loss (distance to open roads); 3) topography, which can affect both locomotion energy and foraging conditions (slope); and 4) an index of either foraging efficiency or security (distance to cover-forage edge). Three of the 4 covariates—DDE, distance to open road, and distance to edge—have analogs in the Wisdom et al. (1986) model, whose improvement was the impetus for our modeling effort (Wisdom et al. 2018a): forage quality, density of open roads, and size and spacing of cover and forage areas. Signs of coefficients and marginal plots of the 3 covariates in our Westside model agreed with relationships hypothesized in the 1986 model, suggesting that these covariates are robust predictors of elk use across time and space in the Westside region (Wisdom et al. 2018a). Elk consistently chose habitat features that maximized energy acquisition and minimized the potential for energy loss and mortality via hunters or poachers, supporting the hypothesis that animals choose habitats that benefit performance (Gaillard et al. 2010). Study designs that link habitat choices to demographic consequences are requisite for improving habitat models for wildlife (Morrison et al. 2012).

Our prediction that nutrition and human disturbance would function as key drivers of elk distributions was corroborated by their strong relation to predicted use (Fig. 21). The model containing only these 2 covariates, though, had a relatively high summed rank (i.e., little support from the data), and Akaike weights for the model approached 0 in all but one modeling area (Appendix D, final set of candidate models). Results from an example application of the regional model in western Washington (example 1 in Wisdom et al. 2018b) supported our prediction that elk use of areas of similar nutrition may be compromised by other, interacting covariates such as human disturbance and topography. In this example, the greatly improved levels of DDE in a local landscape did not translate into increased predicted use because roads remained open following timber harvest (option 3).

Our regional model was successful in predicting habitat use by elk. Multiple lines of evidence suggested that the model was robust, including its top rank in all 5 model development areas (Table 9), high correlation of predicted and observed use in validation with independent telemetry data (Table 11; Appendix E), and consistent trends in covariate values relative to predicted use. This generality, and the successful melding of study-area models into a regional model using a hierarchical, meta-analysis approach, resulted in a large inference space (>11 million ha) compared with that of most ungulate habitat models. In a formal statistical sense, the inference space of the models applies only to the model development and validation areas (Fig. 17; Table 7), which were not selected randomly but opportunistically. These 13 areas, however, were large and encompassed a wide range of environmental conditions, management regimes, and land ownerships across the Westside region.

The meta-analysis approach we adopted allowed for study area (unit-level) summaries that can help clarify the amount of information in the data (Murtaugh 2007); the approach was clearly sufficient in meeting our objectives. Our analysis was generally a more accessible and transparent approach compared to a Bayesian or frequentist hierarchical model. We also attempted to fit a generalized linear mixed model, which would provide estimates of the regional and study area coefficients simultaneously, but that process is not only complicated but also requires additional assumptions about the distribution of the random effects. Moreover, correlation patterns need to be correctly specified within individual modeling areas (Fieberg et al. 2010).

Although modeling results were generally consistent among areas, we found some exceptions, such as elk response to open roads in Pysht (2009) (Figs. 20 and 21). Two Washington State highways were the only roads open to public access in this landscape (Fig. 23), and mean distance to open roads was lowest among all modeling areas (Appendix B, Table B4). Traffic patterns and motorist behavior likely differ between highways

Table 10. Coefficients, confidence intervals (CI), and use ratios for the final Westside habitat-use model for elk in western Oregon and Washington, USA.

Covariate	$\hat{\beta}$	90% CI lower limit	90% CI upper limit	Use ratio
Intercept	-24.2389			
DDE ^a (kcal/g)	7.4772	4.8053	10.1349	111.2% increase for each 0.1-unit increase in DDE
Distance to open road (km)	0.2041	0.0242	0.3252	22.7% increase for each 1-km increase from road
Distance to cover-forage edge (km)	-0.8423	-1.2554	-0.3855	8.1% decrease for each 100-m increase in distance to edge
Mean slope (%)	-0.0545	-0.0630	-0.0441	5.3% decrease for each 1 %-increase in slope

^a DDE = dietary digestible energy.

Table 11. Spearman rank correlation coefficients (r_s) for tests of predicted versus observed use by elk in summer for the regional version of the best habitat-use model (Westside habitat-use model) using 8 model validation data sets from western Oregon and Washington, USA.

Data set (study area and years)	Westside habitat-use model
Coquille North 1991–1992	0.50
Coquille North 1993–1994	0.32
Coquille South 1991–1992	0.87
Coquille South 1993–1994	0.55
Green-Cedar 2006, 2007, 2009	0.99
Makah 2000–2003	0.97
Nooksack 2008–2009	0.96
Quileute 2006–2008	0.97

such as these and less-traveled roads, where drivers may slow down or even stop and leave a vehicle to hike or photograph wildlife. We suspect that elk did not avoid traffic on these highways but responded instead to the high-quality forage on small farms adjacent to them (K. Sager-Fradkin, Lower Elwha Klallam Tribe Natural Resources, personal communication).

For distance to edge, White River 2005 was the only data set with a positive coefficient, indicating higher predicted use farther from edges (Fig. 20). The small sample size in this data set ($n = 6$ elk) may have contributed to the relatively large variability and lack of significance for this covariate. Although the coefficient for distance to edge was negative in Pysht (2009), it was not significant; this site contained extensive private timberland (Appendix A) with many harvest units, and had the shortest average distance to edge among modeling areas (Appendix B, Table B4). Last, the coefficient for DDE was lowest in Green-Cedar 2008, and the lower CI included 0 (Fig. 20). This finding may stem from the overlap of relatively good nutrition with the only open roads in this site (western portion of the area; Fig. 22).

Each covariate in the Westside habitat-use model is strongly supported in published literature. Slope had the largest standardized coefficient among the 4, and its coefficient was the only one for which no CIs spanned 0 in any study area (Fig. 20). Thus, slope remains an important consideration in planning and siting habitat improvements for elk, such as road closures or silvicultural prescriptions, which are best positioned on gentle slopes. Predicted use by elk declined sharply as slope increased from 0 to 40%, with very low probability of use (<0.10) predicted for slopes $>60\%$ (Fig. 21). Preference by elk for gentle to moderate slopes has been documented previously in western Oregon (Witmer 1981, Witmer et al. 1985, Wisdom et al. 1986) and elsewhere (Hershey and Leege 1982, Edge et al. 1987, Johnson et al. 2000, Sawyer et al. 2007). Energetic costs for elk moving on a horizontal plane are nearly 3 times lower than those of moving upslope (Parker et al. 1984), and elk in eastern Oregon preferred to move along ridgelines rather than on steeper slopes perpendicular to drainages (Kie et al. 2005).

Many elk habitat models have included some form of forage variable (e.g., Wisdom et al. 1986, Thomas et al. 1988, Roloff 1998, Johnson et al. 2000, Benkobi et al. 2004), although it has not always been used in model predictions because of the lack of site-specific information needed for its derivation (Cook et al. 1996, Roloff 1998). Earlier studies hypothesized about effects of summer nutrition on population performance of elk in the Pacific Northwest (Trainer 1971, Harper 1987, Merrill et al. 1995), but

only recently have these effects been more widely recognized (Cook et al. 2013, 2018). Moreover, few studies have related distributions of wild elk and performance metrics, such as nutritional condition, to nutritional resources in summer. However, Hebblewhite (2006) demonstrated a positive relation between body mass and pregnancy rates with exposure of elk to high-quality forage, and Middleton et al. (2013a) documented declines in pregnancy rates in migratory elk that they hypothesized were in part a function of declining spring-summer forage conditions. In Montana, Proffitt et al. (2016) found elk exposed to lower summer nutritional conditions entered the winter with lower body fat and pregnancy rates. Summer nutrition for elk, defined in our study by DDE rather than by more commonly obtained forage quality or quantity variables, was a strong and consistent predictor of elk distributions in our Westside habitat-use model. The utility of the nutrition model in strategic land-use planning, not only to predict use but also animal performance, is embodied in the examples described by Wisdom et al. (2018b), which can serve as a template for holistic elk management in the Westside.

Several elk habitat models reflect elk selection for sites close to cover-forage edges, presumably for security (e.g., Wisdom et al. 1986, Thomas et al. 1988, Brunt et al. 1989, Benkobi et al. 2004), although mechanisms for this selection have not been well-described in the literature (Hanley 1983). In western Oregon, 95% of Roosevelt elk locations were within 130 m of cover (Witmer 1981). In Vancouver, British Columbia, more than 50% of Roosevelt elk locations in forage areas were within 40 m of the edge; by contrast, only 20% of locations in cover were within this distance (Brunt et al. 1989). Elk likely select foraging sites close to cover during summer to reduce predation risk or ameliorate effects of micro-climates or insects, and select sites within cover but close to edges to minimize travel to nutritious forage in more open areas and along cover-forage edges (Skovlin et al. 2002). Elk in southwest Oregon shifted to more open vegetation types during a period of controlled road access (Cole et al. 2004), and elk in Yellowstone National Park were closer to forest edges during daytime but did not alter habitat selection in relation to close (within 1 km) encounters with wolves (Middleton et al. 2013b).

Research in Europe on red deer (*Cervus elaphus*; Meisingset et al. 2013) and throughout the range of elk in western North America has demonstrated elk avoidance of roads (Lyon 1979; Cole et al. 1997, 2004; Rowland et al. 2000, 2005; Frair et al. 2008; Ciuti et al. 2012b; Montgomery et al. 2012). Roosevelt elk in the coastal range of Oregon generally avoided all roads in summer, with elk use less than expected within 500 m of paved roads (Witmer 1981, Witmer and deCalesta 1985). Cole et al. (1997) found that elk survival in southwestern Oregon increased, and daily movements and core area size decreased, following road closures, presumably from a decline in poaching and disturbance from traffic. Worldwide, roads represent a dominant anthropogenic feature that can lead to foregone foraging opportunities, increased poaching, and higher energetic costs resulting from flight responses to traffic (Coffin 2007). The strong relation between elk distribution and roads exemplified in our regional model demonstrates its utility in managing elk populations and habitats in relation to road networks throughout the Westside.

Model Validation

The Westside habitat-use model performed extremely well ($r \geq 0.96$) in all but the Coquille study area in southwestern Oregon, where performance was much more variable ($r = 0.32$ – 0.87). Telemetry data from this area were the oldest in our project (early 1990s), and analysis required extensive manipulation of vegetation layers to match the vintage of elk telemetry data (Appendix B). Moreover, elk locations from this study were only diurnal and obtained from VHF collars (mean error ellipse of 1.2 ha), and the sample size was orders of magnitude less than that in other validation data sets (Table 7; Appendix E). Although environmental conditions in Coquille typify those of the southern Oregon Coast Range (Cole et al. 1997), the study area lies at the southern boundary of our modeling region. Landscapes to the south differ substantially, with complex topography, serpentine soils, and flora atypical of much of the Westside (Franklin and Dyrness 1988). Last, road closures established in 1992 for this research only partially limited access (Cole et al. 1997, 2004); thus, we likely under-estimated the extent of open roads in the Coquille data set for 1993–1994. Nonetheless, correlation between predicted and observed elk use in this area was much greater than expected by random chance, indicating the model still performed reasonably well given the limitations of the data. Including this study area was useful because it represented the only data from Oregon, and its location at the boundary of the Westside region offered insights about how robust our validation results might be to higher location error, lower relocation frequency, and unknown fix rate.

A possible contribution to the strong performance of some of our validation data sets may be the spatial overlap of certain areas used for model development versus validation (e.g., Green-Cedar and White River; Fig. 17). Although some of these areas overlapped and thus were not completely spatially independent, model development versus validation data sets always differed by the year in which telemetry data were collected and across years by collared animals from which telemetry data were obtained. Thus, we did not use any individuals for both model development and validation. Moreover, using independent data for model validation is preferred over other methods such as cross-validation or other methods of sub-setting the original data, which may lead to inflated measures of model performance (Johnson 2001).

Sources of Uncertainty in Model Application

We developed competing models based on a combination of ecological rationale, biological hypotheses, and predictions, a structured process for model development, and mechanistic covariates related to energy balance to evaluate habitat use. Such an approach provides a useful modeling framework for advancing knowledge about a species' habitat use and requirements (Morrison 2001, 2012). We included a covariate, DDE, in our habitat-use model that was the response variable of the best nutrition model. Thus we modeled a model, which can compound estimation and prediction errors (Mowrer and Congalton 2000). We used coarse-scale GIS layers as source data (Appendix B), often criticized as having insufficient or unknown accuracy for modeling (Shao and Wu 2008). The spatial resolution, extent, and classification of coarse-scale data to estimate, map, and validate habitat-use and

resource-selection models can affect modeling results or their interpretation (Morris et al. 2016). These approaches could lead to an inability to detect causal relationships and represent them in habitat-use modeling. However, our modeling produced ecologically meaningful results (i.e., not detecting anticipated results that could be Type II errors) and no unexpected results (i.e., spurious results that could be Type I errors).

Our regional model predictions reflect relations between elk and current environmental conditions. How climate change or other processes might affect these predictions, specifically those derived from vegetation-based covariates (distance to edge and DDE), has not been tested. Predicted regional increases in annual temperatures (projected to be highest in summer) of 1.8°C to 5.4°C by 2070–2099 in the Pacific Northwest, coupled with projected 30% decreases in summer precipitation (Mote et al. 2014), will undoubtedly affect forage phenology and associated biomass and quality of forage for elk. However, relative, if not absolute, values of nutrition for elk as predicted by the nutrition model should remain robust, as noted by Cook et al. (2018). Most research to date evaluating impacts of climate change on ungulates does not specifically address habitat use or distributions but rather population dynamics, especially in relation to winter severity (e.g., Patterson and Power 2002, Hebblewhite 2005). Thus these studies are not directly relevant to our summer habitat-use model. Wang et al. (2002), however, evaluated potential impacts of climate change on elk populations in Rocky Mountain National Park in Colorado, USA, and projected that higher summer temperatures would slow population growth in elk. Given the uncertainty of future climate, land management regimes, and other processes such as abundance of invasive plant species, insects, and wildfire, an adaptive management approach will be required to understand best and appropriate applications of our habitat-use model and to guide future research as needed (Wisdom et al. 2018b).

We did not incorporate the presence or density of predators as predictors in our habitat-use model, primarily because such data were unavailable across our study areas. Despite this omission, the model performed well in predicting current elk distributions. However, we recognize such data can play an important role in modeling the full suite of functional habitat components that may affect elk distributions (Gaillard et al. 2010). Two common Westside carnivores are known predators of elk. Black bears prey primarily on neonate elk (Zager and Beecham 2006, Griffin et al. 2011), whereas cougars prey primarily on elk calves during summer but also will kill adult elk (White et al. 2011a, Clark et al. 2014). If Westside elk do respond to the presence of cougars and black bears, that response is likely reflected in their current distributions because they have shared ranges with these 2 common predators for decades. Moreover, predation by black bears occurs during such a brief temporal window and on calves, which we did not monitor, that adult elk are unlikely to respond to bears at the scale of our models. Similarly, cougars are cryptic predators whose presence may not affect summer elk habitat use at the temporal and spatial scales of our models. For example, birth-site selection of Rocky Mountain elk at larger spatial scales did not appear to be influenced by predation risk but rather by access to nutritional resources (Rearden et al. 2011), which we accounted for in our models. We know of no published literature

documenting changes in habitat use by elk in response to either of these 2 predators.

Gray wolves were functionally absent in the Westside region during the years in which our data were collected. Wolves are actively colonizing Washington and Oregon through dispersal from populations in British Columbia, Idaho, and Montana (Oregon Department of Fish and Wildlife 2010, Washington Department of Fish and Wildlife, Confederated Colville Tribes, Spokane Tribe of Indians, USDA-APHIS Wildlife Services, and U.S. Fish and Wildlife Service 2017). Currently, there is one pack located just east of our modeling region in Washington (Teanaway; Washington Department of Fish and Wildlife, Confederated Colville Tribes, Spokane Tribe of Indians, USDA-APHIS Wildlife Services, and U.S. Fish and Wildlife Service 2017). No packs have been established within the Westside region in Oregon; however, a pair of wolves was documented in early 2018 in southern Wasco County, Oregon, in the Cascade Mountains (Oregon Department of Fish and Wildlife 2018). In contrast to evidence for cougars and bears, wolves can effect changes in elk distributions and habitat use, often with negative consequences for fitness (Frair et al. 2005, Hebblewhite et al. 2005, Mao et al. 2005, Muhly et al. 2010, White et al. 2012). These results, however, are inconsistent (Middleton et al. 2013*b*). If wolves become sufficiently abundant in the Westside, recalibration of the habitat-use model could be required through additional research, although habitat shifts in response to wolves have been most often reported for winter, not summer, and included use of steeper slopes, higher elevations, and denser cover (Mao et al. 2005). Moreover, in some situations, human disturbance (e.g., hunting, other recreation, high-volume traffic on roads) may exert stronger effects on elk habitat use than do wolves (Proffitt et al. 2009, Ciuti et al. 2012*b*). Thus, the inclusion of a roads covariate in our habitat-use model may provide some resilience of the model even with the projected re-establishment of wolves in western Oregon and Washington.

MANAGEMENT IMPLICATIONS

The habitat-use model predicts relative probability of use by elk, and can guide management treatments to improve elk habitat quality and distributions, such as increasing use on national forest lands relative to adjacent land ownerships. It is not a carrying-capacity model, nor is it a model to predict population numerical response. Such models require intensive data about amount and quality of forage and many assumptions about animal density and other factors that may limit the ability of a landscape to support a defined number of animals (Hobbs and Swift 1985, Beck et al. 2006, Cook et al. 2016). However, Vales et al. (2017) successfully applied equations in our Westside nutrition model to create an elk forage index on lands managed by the Muckleshoot Indian Tribe in central Washington. The scale-independent index is intended to guide timber harvest management and reflects the density of female elk that a given landscape can support. Similarly, Roloff (1998:158) developed a habitat potential model for elk that reflects the “inherent ability of the landscape to produce and sustain elk in the absence of human disturbance.” Our model integrates nutrition with human disturbance and other factors to predict relative—but not absolute—use by elk within the analysis area.

For successful application of the model, users should understand its multivariable framework. For example, silvicultural treatments to improve nutritional conditions for elk may yield negligible benefits in term of increased elk use in sites with high open road densities or steep slopes (see Wisdom et al. [2018*b*] for specific examples). Similarly, closing roads in locales with relatively low DDE and limited opportunity to improve nutrition through thinning may be futile if managers seek to improve elk habitat, distribution, or elk performance. Wisdom et al. (2018*b*) describe specific applications of the nutrition and regional habitat-use model, and offer caveats and suggestions for management application in the Westside region.

Nutrition and Habitat-Use Models for Elk Management in Western Oregon and Washington

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INTRODUCTION

Landscape modeling of habitat use by wide-ranging animal species such as elk is a topic of increasing focus in the wildlife profession (Ciuti et al. 2012a, b; Nielson and Sawyer 2013). Models of habitat use, or related models of resource selection, predict the probability of animal use of a given area and time based on a wide range of environmental covariates (Rowland et al. 2018). These models can provide valuable knowledge about a species' habitat choices in time and space that presumably index the species' habitat needs (Gaillard et al. 2010, Hebblewhite and Haydon 2010). Models are particularly useful when they are based on covariates that are ecologically meaningful to the species' habitat requirements and that can be directly manipulated by managers to achieve desired changes in a species' habitat use, distribution, and performance (mechanistic covariates; Wisdom et al. 2018a).

We describe and demonstrate the management utility of elk nutrition and habitat-use models developed and validated for applications in western Oregon and Washington (Westside; Cook et al. 2018, Rowland et al. 2018). We first summarize intended management applications and considerations, with focus on interpretation of predictions and spatial and temporal scales of use. We then provide management examples that highlight types of applications and benefits. Finally, we discuss challenges and implications of elk modeling in the Westside region, given current management direction on different land ownerships, stakeholder involvement, and future sources of management and environmental uncertainty.

Management Applications and Predictions

The nutrition and habitat-use models evaluate summer range during June–August, a period of nutritional stress for lactating female elk in the Westside region (Cook et al. 2018). Explicit rationale and empirical support for evaluating summer range was

detailed by Cook et al. (2004, 2013, 2016, 2018). Evaluation of the nutrition model, which showed the strong positive relationship between landscape composition of summer predictions of DDE (kcal/g) and pregnancy rates and body fat of associated elk populations, supported the focus on summer as a period of nutritional limitation in the Westside region (Cook et al. 2018). These relationships further justified the focus on modeling habitat use during summer on Westside landscapes (Rowland et al. 2018).

The nutrition model predicted DDE during summer in the Westside region using a combination of covariates, including PNV zone, overstory canopy cover, and hardwood composition (Cook et al. 2018). Model predictions were evaluated with independent data on selection ratios, elk performance, and habitat use. Results supported the predictions that fine-scale nutrition data (i.e., DDE) collected with captive elk represent the actual nutrition levels of wild elk, and that these levels can be re-scaled to produce reasonably accurate, broad-scale predictions of nutrition across the Westside region (Cook et al. 2018).

The habitat-use model predicted the relative probability of elk use on Westside landscapes during summer (Rowland et al. 2018). Predictions were based on 4 covariates: DDE outputs from the nutrition model and 3 non-nutrition covariates (distance to open roads, slope, and distance to cover-forage edge; Rowland et al. 2018). The 4 covariates best predicted use by elk across the Westside region at landscape scales based on data from multiple study areas used for model development. Model predictions were validated with independent data on habitat use from additional study areas not included in model development (Rowland et al. 2018). Results supported the hypotheses that elk use of landscapes is consistent across the Westside region, as captured in 1 regional model; and that the regional model would include “a suite of interacting covariates related to elk energy balance” often found to account for elk use in prior research (Rowland et al. 2018:32).

The nutrition and habitat-use models, when used together, predict elk nutrition, habitat use, elk distribution, and

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performance at landscape scales of direct relevance to elk management (Fig. 2; Wisdom et al. 2018a). The nutrition model predicts the spatial distribution of nutritional resources (Cook et al. 2018); the habitat-use model can predict the extent to which those resources will be used (Rowland et al. 2018). Landscapes managed for nutrition therefore require simultaneous management of non-nutrition covariates to facilitate desired nutritional use. Effective management thus relies on both models (see Management Examples).

The nutrition and habitat-use models further predict landscape distribution (Rowland et al. 2018) and performance (Cook et al. 2018) of elk populations. Landscape distribution is estimated by summing the predictions of relative probabilities of habitat use across different management boundaries of interest, such as land ownerships (see Management Examples). Animal performance is predicted by regression equations showing that pregnancy rates and body fat of lactating female elk increase in response to increasing landscape area of higher levels of DDE in Westside elk populations (Cook et al. 2018). Increasing animal performance based on increasing area of higher nutrition, however, implicitly assumes that such areas will be used by elk, as predicted by the habitat-use model (Rowland et al. 2018). Our management examples demonstrate these model uses.

METHODS

Scales of Application

Nutrition model.— The nutrition model can be applied in 2 ways: spatially explicit or tabular. Equations in the model to predict forage biomass and DDE are the same for both applications (Cook et al. 2018). Spatially explicit model application can occur at any spatial scale of interest, ranging from an individual stand to the entire Westside region. Applying the model at a stand level requires accurate field data that reflect site-specific conditions (Cook et al. 2018). By contrast, coarse-scale GIS data are often sufficient (Appendix B) for applying the nutrition model over large landscapes like those in which the nutrition and habitat-use models were developed and validated (Appendix A).

The tabular application is not scale-dependent but instead can be used in gaming scenarios to understand potential effects on DDE values of changes in overstory canopy cover and hardwood composition in a given PNV zone (Vales et al. 2017, Cook et al. 2018). For example, a manager may want to evaluate how nutrition differs under 4 timber harvest prescriptions in conifer stands that reduce canopy cover to 0%, 20%, 40%, and 60% with either constant or varying levels of hardwood composition (Table 12). For the

tabular application, estimates of canopy cover and hardwood composition can be used to drive the model, first to predict forage biomass and then DDE, although estimates of forage biomass (i.e., selected, neutral, accepted) derived directly from field sampling in the stands would provide more accurate predictions of DDE.

For landscape assessments, the spatially explicit form of the nutrition model can be used to predict DDE as a stand-alone evaluation or in tandem with predictions from the habitat-use model. Applying the habitat-use model by definition requires first applying the nutrition model because DDE predictions are a required covariate in the habitat-use model (Rowland et al. 2013, 2018). When using the nutrition model as a stand-alone tool for landscape assessment, the size of area should be large enough to affect conditions for a local population. Minimum size should be approximately 800–1,000 ha (Rowland et al. 2013), which equates roughly to the area of summer home ranges of elk in the Westside region (Cole et al. 1997, McCorquodale 2003, Witmer et al. 1985, Wisdom et al. 1986).

Predictions of the nutrition model are made to each pixel (grid cell) within an analysis area. Results are directly comparable across all pixels in the analysis area, and across different analysis areas for a given time period (Cook et al. 2018). Results from the spatially explicit nutrition model can then be used to predict pregnancy rates and body fat of lactating female elk in a given summer range, based on the percentage of the analysis area occurring in the higher nutritional classes of DDE (Figs. 12 and 13; Cook et al. 2018), as demonstrated in our management examples.

Habitat-use model.— Assessing habitat use involves 2 general steps. The first is applying the habitat-use model in an area of $\geq 10,000$ ha, referred to as a regional landscape. This scale is compatible with the range of study area sizes used to develop and validate our models (Appendix A; Cook et al. 2018, Rowland et al. 2018). Areas $\geq 10,000$ ha also encompass multiple populations of summering elk, thus providing an appropriate area in which to evaluate summer range conditions at a regional scale.

The specific size and boundaries of a regional landscape depend on objectives (Rowland et al. 2013). Smaller regional landscapes might be appropriate for focusing on habitat conditions in a given land ownership or drainage (see Example 1). Larger regional landscapes might be appropriate for evaluating conditions across multiple land ownerships that encompass cumulative management activities at large spatial extents (see Example 2).

After the boundary of the regional landscape is established, a 4-km buffer must be placed around the boundary before applying the habitat-use model (see Management Examples). All roads open to public motorized use are to be mapped within this buffer, as are all cover-forage edges (Rowland et al. 2013, 2018). Open roads and cover-forage edges outside the analysis areas but within the 4-km buffer may affect elk use within the analysis areas and thus should be considered (Rowland et al. 2013, 2018).

A second, optional step beyond assessment of a regional landscape is a summary of results for smaller areas, referred to as local landscapes, which are embedded within the regional landscape. In this case, results from applying the habitat-use model for the regional landscape are subsetted to evaluate local conditions or projects, as defined by boundaries of the local landscape. The minimum area for designating a local landscape is

Table 12. Dietary digestible energy (kcal/g) of forage for elk in relation to example levels of overstory canopy cover and hardwood composition of coniferous forests in the Pacific silver fir–mountain hemlock potential natural vegetation zone of the Westside region, western Oregon and Washington, USA, based on the elk nutrition model (Cook et al. 2018).

Hardwood composition	Overstory canopy cover			
	0%	20%	40%	60%
0%	2.93	2.84	2.74	2.63
5%	2.94	2.86	2.76	2.66
10%	2.95	2.88	2.78	2.68
20%	2.96	2.92	2.82	2.72
50%	3.00	3.03	2.95	2.86

800–1,000 ha; this size is compatible with summer home ranges for elk in the Westside region as described earlier, and reflects a scale of management that would be ecologically meaningful to a local population of elk. This is the same minimum area for applying the nutrition model as a stand-alone landscape assessment. Changes in pregnancy rates and body fat of lactating elk associated with management actions to improve nutrition are thus assessed over an area large enough to affect a population and ensure that associated changes in use in response to changes in nutrition are evaluated at a meaningful scale. Similarly, changes in elk distribution in response to habitat management are summarized at this same scale in which the distribution of a population may be affected (see Management Examples).

Habitat-use modeling does not require the designation or analysis of local landscapes, and their inclusion depends on objectives. Once local management projects are identified (e.g., specific timber harvest units or new road network) as the basis for establishing boundaries of a local landscape, a buffer distance of approximately 1.6 km should be placed around those project areas for summarizing habitat use (see Example Management Uses). The buffer accounts for the effects of the distance to cover-forage edge covariate on elk use, based on the new edges created from timber harvest units or other changes to forest structure (Rowland et al. 2013).

Habitat-use model predictions (Rowland et al. 2013, 2018) are made for each pixel within a regional landscape. Predictions are not standardized on a 0 to 1 scale but are relative to all other values in the area in which the habitat-use model was applied. It is possible to standardize these predictions but they remain relative to other values within the area, and are not directly comparable to predictions made during separate model runs for other areas (although patterns of predicted use may be compared

qualitatively between different regional landscapes). Thus, the key to making predictions of elk use comparable across a landscape of interest is to apply the model over the entire area. This point illustrates the benefits of applying the model over a larger regional landscape versus a smaller one: results are comparable across the entire area in which the model is applied, and can be subsetted to any local landscapes of interest. Similarly, model results are comparable across time periods but only when the regional landscape boundary is constant across time periods (Rowland et al. 2013).

Management Examples

We provide 2 examples to demonstrate nutrition and habitat-use modeling applications for landscape management. Example 1 considers 3 management options within 1 land ownership to evaluate effects of proposed silvicultural prescriptions and management of open roads. This example highlights the complementary use of results at scales of regional and local landscapes. Example 2 is an evaluation of multiple land ownerships to quantify and understand elk distribution across ownerships. Results can be used to establish and implement broad-scale objectives for elk distribution and performance (pregnancy rates and body fat of females).

For both examples, we highlight key results and management interpretations but do not address details of how to apply the models in a GIS framework. Rowland et al. (2013) describe and illustrate these details, give additional examples for data summary and display, and provide information about using spatial data sets needed to derive model covariates. The Westside elk modeling website provides downloadable GIS programs to apply the models and example data layers (<https://www.fs.fed.us/pnw/research/elk/toolbox/index.shtml>). Doerr (2016) and Vales et al. (2017) provide

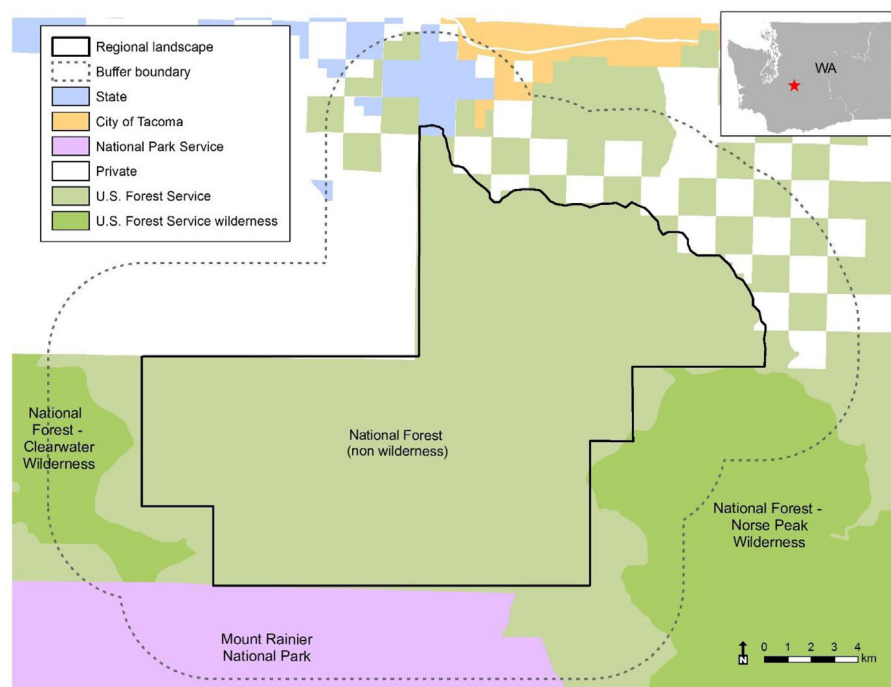


Figure 27. Example 1 study area (27,980 ha) in the White River drainage of western Washington, USA (see upper right inset) showing land ownership and allocations present in 2010 that were used to estimate current conditions for example 1.

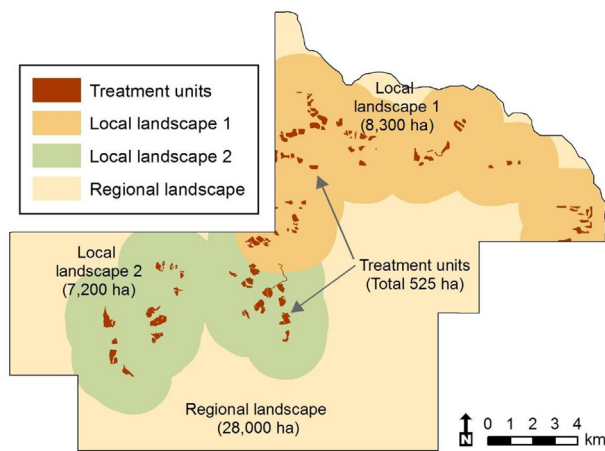


Figure 28. Example 1 had 3 management options. Option 1 included 256 ha of clearcut regeneration harvest in 61 units within local landscape 1 plus 269 ha of commercial thinning in 46 units within local landscape 2. Option 2 included commercial timber harvest on the same units as option 1, except that all units will be clearcut (no commercial thinning). Option 3 was the same as option 2 except 71 km of roads closed as part of timber harvest remained open.

additional examples of applying the Westside models, which complement those provided here. Our examples use land ownerships and environmental conditions for 2010 as the reference or base condition (Appendix B).

Example 1.—The first example encompasses 27,980 ha in the White River drainage of western Washington within the Mt. Baker-Snoqualmie National Forest and adjacent areas of the Wenatchee National Forest (Fig. 27). The area overlaps portions of the White River study areas where telemetry data on elk were obtained for habitat-use modeling (Appendix A). The example is based on discussions and management decisions made between Forest Service managers and the Muckleshoot Indian Tribe on ways to improve elk nutrition and habitat use in the area (USDA Forest Service 2001a, b). These management options were formally evaluated by Forest Service managers as a result of these discussions (USDA Forest Service 2001a, b), and implementation of option 1 began in 2012 (USDA Forest Service 2012a, b).

Different combinations of forest silvicultural prescriptions and management of open roads were considered under 3 management options (Fig. 28). This illustrates the effects of proposed

management within 1 land ownership, and how results for regional and local landscapes can be used in complementary ways.

We identified 61 forested units encompassing 256 ha (mean unit size = 4.2 ha, range = 0.3–12.3 ha) for timber harvest under option 1, based on clearcutting as the harvest regeneration method (local landscape 1; Fig. 28). We identified 46 additional units encompassing 269 ha (mean unit size = 5.8 ha, range = 0.3–23.1 ha) for commercial thinning under this option (local landscape 2; Fig. 28). Overstory canopy cover would be reduced from >70% before timber harvest to 0% after clearcutting and to 60% after commercial thinning.

Option 2 included commercial timber harvest on the same units as option 1, except that all units in local landscape 2 would use clearcut regeneration harvest (i.e., no commercial thinning). Option 3 included the same units and silvicultural treatments as option 2 but differed in road management. Under option 3, 71 km of roads used for log hauling would remain open to public motorized use after timber harvest but would be closed under options 1 and 2 (Fig. 29).

For example 1, we selected the boundaries of the regional landscape to evaluate the 3 management options at a regional extent encompassing all national forest management activities and lands that could be managed with active silviculture (non-wilderness areas of national forest). Boundaries of the regional landscape thus followed national forest boundaries with private and state lands to the north, wilderness or roadless areas to the east and west, and NPS lands to the south (Fig. 27). We included a 4-km buffer beyond the boundaries to accurately evaluate distance to open roads and cover-forage edges within the regional landscape, as described earlier.

We selected the boundaries of the 2 local landscapes to evaluate smaller areas adjacent to proposed harvest units (Fig. 27). We established boundaries using a 1.6-km buffer around the harvest units to evaluate spatial effects on elk use in relation to distance to cover-forage edges created during timber harvest. This buffering distance for summarizing habitat use in a local landscape was supported by results from the distance to cover-forage edge covariate in the habitat-use model; most elk use occurred within 1.6 km from an edge.

Example 2.—The second example encompasses 94,403 ha in the White River drainage of western Washington (Fig. 30). This area includes portions of the White River study areas

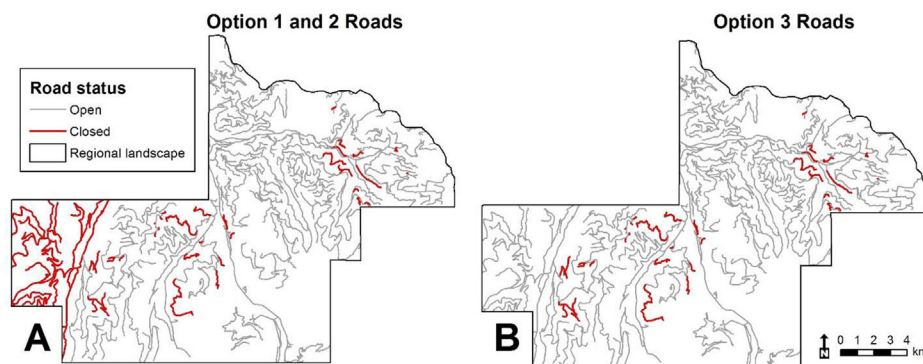


Figure 29. Roads open versus closed to public motorized use under options 1 and 2 (A) versus under option 3 (B) for example 1. Approximately 71 km of roads in the western part of the regional landscape would remain open after timber harvest under option 3. However, the majority of roads (524 km) remain open to public motorized use under all 3 options.

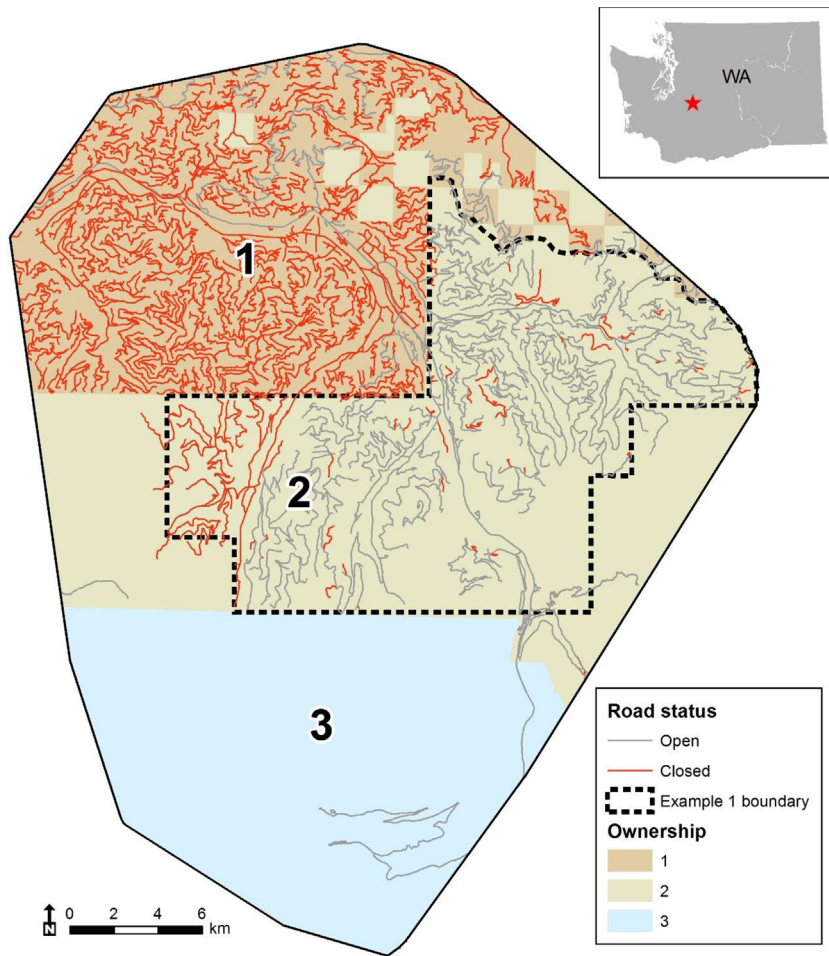


Figure 30. Year 2010 land ownership in the 94,403-ha area of example 2, composed of 3 major ownerships: private industrial forest (ownership 1), Mt. Baker-Snoqualmie and Wenatchee National Forests (ownership 2), and Mount Rainier National Park (ownership 3), Washington, USA. Ownership 1 included a small percentage of state lands because small tracts of state lands were interspersed among large areas of private industrial forest. Example 1 lies entirely within example 2, as outlined in dotted lines. Roads open versus closed to public motorized varied widely by land ownership.

where elk telemetry data were analyzed as part of habitat-use modeling (Appendix A). It encompasses the entire portion of national forest included in example 1, as well as private industrial forest and state lands to the north and Mount Rainier National Park to the south (Fig. 30). The Mt. Baker-Snoqualmie and Wenatchee National Forests compose 45% of the area, followed by Mount Rainier National Park (26%) and private industrial forest (24%). State lands compose the remaining 5%, which is sparsely distributed among private industrial forest and thus is combined with surrounding private industrial forest for our analysis. Estimation of model covariates in our examples used the same environmental data that we used to derive covariates for model development in the White River study areas (Appendices A and B).

RESULTS

Nutrition Predictions, Example 1

Over 85% of the regional and local landscapes under the existing condition in Example 1 are composed of the 2 lowest nutrition classes, poor and low-marginal (DDE <2.58 kcal/g; Tables 2 and 13; Fig. 31). These classes represent conditions below basic requirement of lactating female elk during summer and are

associated with lowest levels of female body fat and pregnancy rates (Cook et al. 2018).

The 4 highest nutrition classes (classes 3–6) composed 14.2% of the regional landscape and 12.4% and 13.6% of the 2 local landscapes under the base (existing) condition (Table 13; Fig. 31). These classes represent levels of nutrition that meet or exceed the basic requirement of lactating female elk during summer (Cook et al. 2018). The 3 highest nutrition classes (classes 4–6; Table 2) exceed basic requirement and composed 5.9% of the regional landscape and approximately 6% of each of the 2 local landscapes under the base (existing) condition (Fig. 31; Table 13).

For the regional landscape, the proposed silvicultural treatments would increase the area of DDE in classes 3–6 from 14.2% currently to 15.7% and 16.5% under options 1 and 2, respectively (Table 13). The proposed treatments also would increase the regional landscape area of DDE in classes 4–6 from 5.9% currently to 6.9% and 8.3% under options 1 and 2 (Table 13).

Nutrition classes 3–6 (high-marginal to excellent; Table 2) capture levels of DDE in which pregnancy rates are responsive to nutritional change (Table 13). Similarly, nutrition classes 4–6 (low-good to excellent; Table 2) capture levels of DDE that affect percent body fat of lactating female elk (Table 13). For the

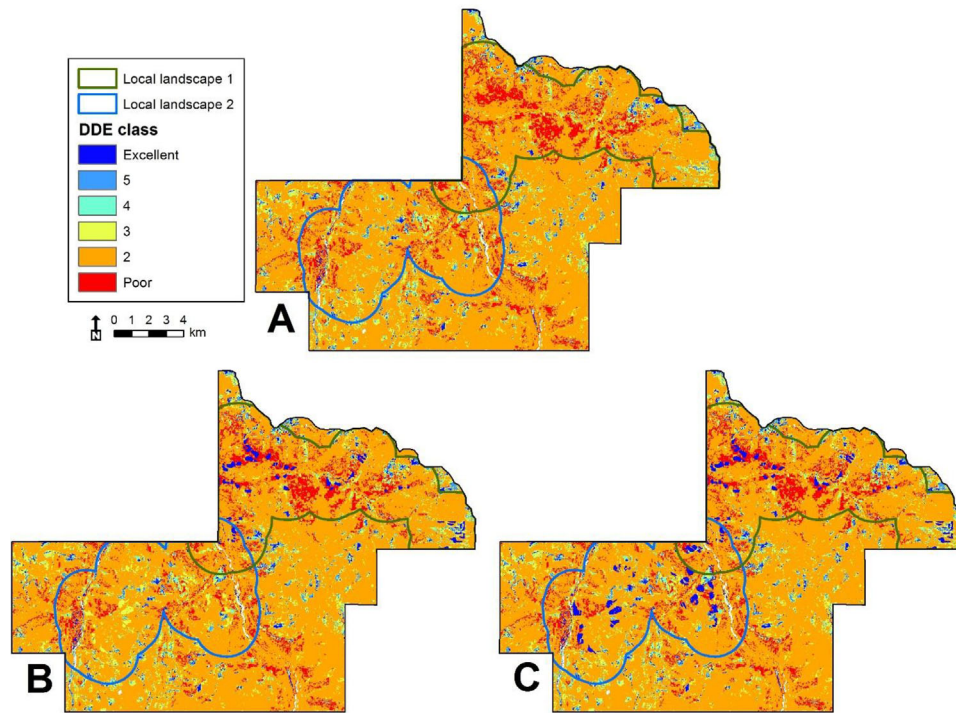


Figure 31. Six classes of elk nutrition in the White River drainage of western Washington, USA for the base condition (A), option 1 (B), and options 2 and 3 (C) for example 1. Land ownerships and environmental conditions for 2010 were used as the base condition (Appendix B).

regional landscape, the increased area of nutrition classes 3–6 is predicted to increase pregnancy rates for lactating female elk from 0.63 currently to 0.68 under option 1 and 0.71 under option 2, using the equation for percent area in DDE >2.58 kcal/g (Fig. 12C; Table 13). Similarly, the increased area of nutrition classes 4–6 is predicted to increase percent body fat in lactating female elk on the regional landscape from 9% currently to 10% under both options, using the equation for percent area in DDE >2.75 kcal/g (Fig. 13; Table 13). Silvicultural treatments and nutritional results for option 3 are the same as option 2 for the regional landscape.

Although the predicted improvements in pregnancy rates and body fat under options 1 and 2 may appear biologically insignificant, these improvements are substantial in relation to the small land area treated: only 1.9% of the regional landscape is being treated silviculturally under these options to achieve the improvements. These results suggest that even a slightly higher percentage of land area treated silviculturally to improve nutrition (e.g., 3–4% of the regional landscape) for option 2 would result in a substantial increase in pregnancy rates and body fat. For example, a 4% increase in area of nutrition classes 3–6 above that for option 2 in the regional landscape

Table 13. Percent area by dietary digestible energy (DDE) class for the regional landscape and 2 local landscapes for the current time period (base) and under 3 management options presented for example 1, and the predicted pregnancy rate and body fat for lactating female elk based on the percent area of DDE in nutrition classes 3–6^a and 4–6^b, respectively (Cook et al. 2018). We used year 2010 conditions for base.

	DDE class ^c						Pregnancy rate (%)	Body fat (%)
	1	2	3	4	5	6		
Regional landscape								
Base	9.1	76.6	8.3	2.4	1.9	1.6	0.63	9
Option 1	8.6	75.7	8.8	2.4	1.9	2.6	0.68	9
Option 2 and 3	8.6	74.9	8.2	2.4	1.9	4.0	0.71	10
Local landscape 1								
Base	15.8	71.9	6.8	2.6	1.5	1.5	0.56	9
Option 1	14.6	69.9	6.7	2.5	1.5	4.8	0.67	10
Option 2 and 3	14.6	69.9	6.7	2.5	1.5	4.8	0.67	10
Local landscape 2								
Base	10.2	76.2	7.6	2.8	1.6	1.6	0.60	9
Option 1	9.5	74.6	9.7	2.8	1.6	1.8	0.69	9
Option 2 and 3	9.5	71.4	7.5	2.8	1.6	7.2	0.78	11

^a Equation for predicting pregnancy rates of lactating female elk (Y), where x = % area with DDE >2.58 kcal/g and $y = e^{(-1.709 + 0.157x)} / 1 + e^{(-1.709 + 0.157x)}$.

^b Equation for predicting percent body fat of lactating female elk (Y), where x = % area with DDE >2.75 kcal/g and $y = 6.1 + 0.43x$. For landscapes with 0% area of DDE >2.75 kcal/g, percent body fat = 6.1%, which is the Y intercept of above equation. Predictions of body fat are capped at 15% when using this equation because of limitations in inference in making body fat predictions at higher levels.

^c The DDE values (kcal/g) for classes were 1 = <2.40; 2 = 2.40–2.58; 3 = >2.58–2.75; 4 = >2.75–2.83; 5 = >2.83–2.90; 6 = >2.90.

would increase pregnancy rates from the baseline of 0.63 currently to 0.81; this level of increase is biologically significant (Proffitt et al. 2016).

The shifts to higher nutrition classes are primarily from class 2 to class 3 under option 1, and from class 2 to class 6 under option 2 (Table 13). Thus, the nutritional change under option 2 shifts more area to the highest nutritional class than option 1. Superior nutrition under option 2 is due to clearcutting used as the silvicultural approach for timber harvest, which provides the lowest canopy cover and highest nutritional response (Table 12; Cook et al. 2018). Nutritional results for option 3 are the same as option 2.

Nutritional improvements and effects on pregnancy rates and body fat within the 2 local landscapes illustrate the additional, positive effects of silviculture (Table 13). On local landscape 1, the percent area of DDE in classes 3–6 would increase from 12.4% currently to 15.5% under options 1 and 2 (Table 13); the percent area of DDE in classes 4–6 would increase from 5.6% currently to 8.8% under options 1 and 2 (Table 13). The increased area of better nutrition classes in local landscape 1 is predicted to increase pregnancy rates for lactating female elk from 0.56 currently to 0.67, and increase percent body fat from 9% to 10% under both options (Figs. 12 and 13; Table 13). Changes in pregnancy rates and percent body fat of female elk on local landscape 2 resulting from option 2 are superior to those of local landscape 1 (Table 13). The higher pregnancy rates and body fat predicted on local landscape 2 under option 2 reflect the larger area of clearcutting resulting in a greater spatial shift to the highest nutrition class (class 6; Table 13). Nutritional results for option 3 are the same as option 2.

As with results for the regional landscape, nutritional increases for local landscape 2 are superior for option 2 versus 1 because

clearcutting was used as the regeneration method compared to commercial thinning under option 1. Clearcutting produces an overhead canopy cover of 0%, which yields the highest increase in DDE (Cook et al. 2018). Clearcutting under option 2 thus results in substantially higher levels of DDE, with the most increase in the highest nutrition class (class 6; Fig. 31; Table 13).

Commercial thinning under option 1 does not reduce overhead canopy cover sufficiently to detect a measureable increase in higher nutrition classes and associated animal performance compared to the base condition (Table 13). Canopy cover levels of 40% or 60%, often associated with commercial thinning under the Northwest Forest Plan (USDA Forest Service and USDI Bureau of Land Management 1994*a, b*), yield substantially lower levels of DDE compared to an overhead canopy cover of 0% that is associated with clearcutting (Table 12).

Interpreting the nutritional improvements and their predicted benefits to pregnancy rates and body fat of females in local landscapes 1 and 2 are similar to those for the regional landscape. Specifically, only small percentages of the landscapes are being treated silviculturally to improve nutrition. Resulting improvements in pregnancy rates and body fat are apparent, but their biological significance could be increased substantially with even a slight increase in areas treated silviculturally beyond the levels treated in local landscapes 1 and 2.

Habitat-Use Predictions, Example 1

Elk use (relative probability of use) is predicted to increase under options 1 and 2, with increased use concentrated in the 2 local landscapes that encompass the proposed silvicultural treatments (Figs. 32 and 33). For options 1 and 2, the proposed silvicultural activities required motorized road access, and 109 km of these roads

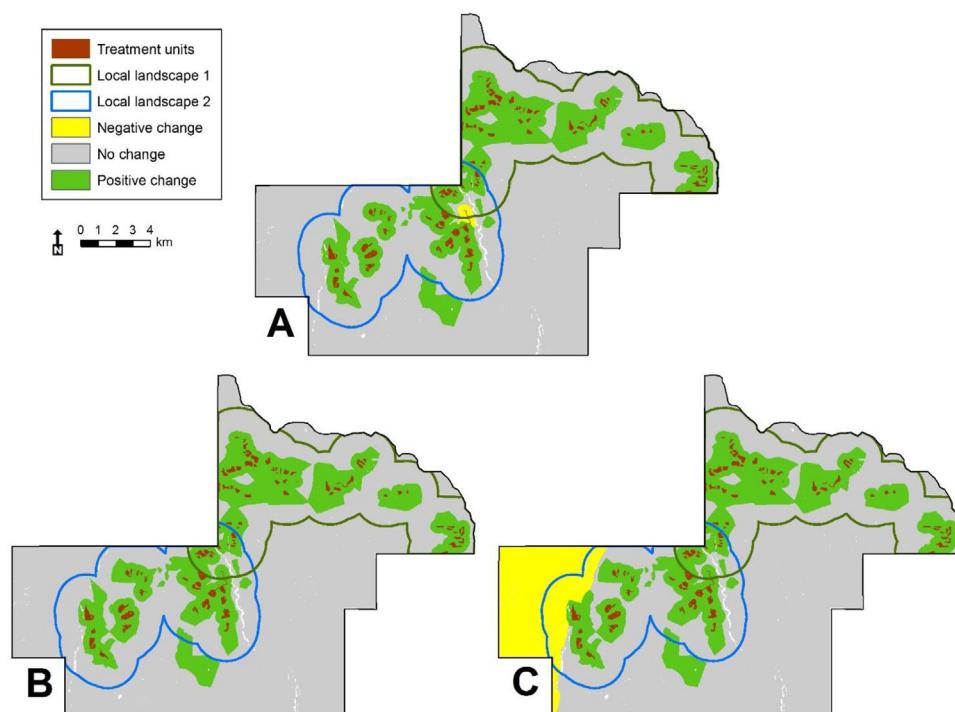


Figure 32. Areas shown as increasing, decreasing, or remaining the same for predicted elk use in the White River drainage of western Washington, USA under option 1 (A), option 2 (B), and option 3 (C) in example 1.

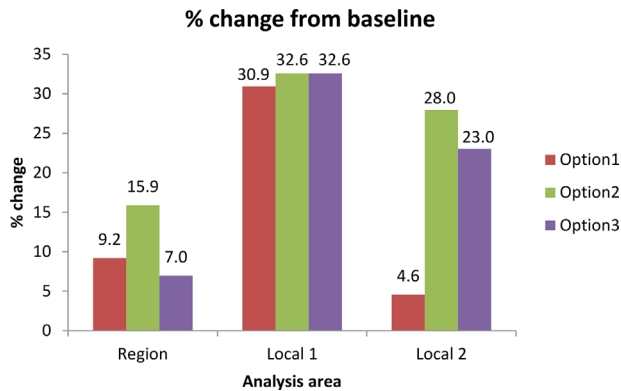


Figure 33. Percent change in relative probability of elk use in the White River drainage of western Washington, USA under each management option relative to the base condition under example 1, as summarized for the regional landscape (region) and local landscapes 1 and 2 (local 1, local 2).

would be closed to public motorized use after timber harvest. For option 3, 71 km of the roads closed under options 1 and 2, providing access to areas of timber harvest, would remain open to public motorized use after harvest. As a result, the predicted increase in elk use is diminished under option 3 compared to options 1 and 2 for

the regional landscape, despite the increased nutrition provided by timber harvest (Figs. 32 and 33).

Many of the predicted increases in elk use are substantial: >30% increase in elk use in local landscape 1 under all options, a 28% and 23% increase in local landscape 2 under options 2 and 3, and a 16% increase in use in the regional landscape under option 2 (Fig. 33). The increase in predicted elk use relative to the existing condition was higher for option 2 than for 1 for both the regional landscape and local landscape 2 because clearcutting was the form of timber harvest under option 2 versus commercial thinning under option 1 (Fig. 33). Predicted elk use under option 2 also is higher than option 3 for the regional landscape and local landscape 2, owing to the road closures implemented under option 2 compared to 3 (Fig. 33).

Nutrition Predictions, Example 2

The 3 major land ownerships in the White River under example 2 provide a strong contrast in nutritional conditions (Fig. 34). Private industrial forest supported highest levels of nutrition, followed by Mount Rainier National Park. These 2 land ownerships had 39.4% and 28.4% of their respective areas in nutrition classes 3–6, which are associated with predicted

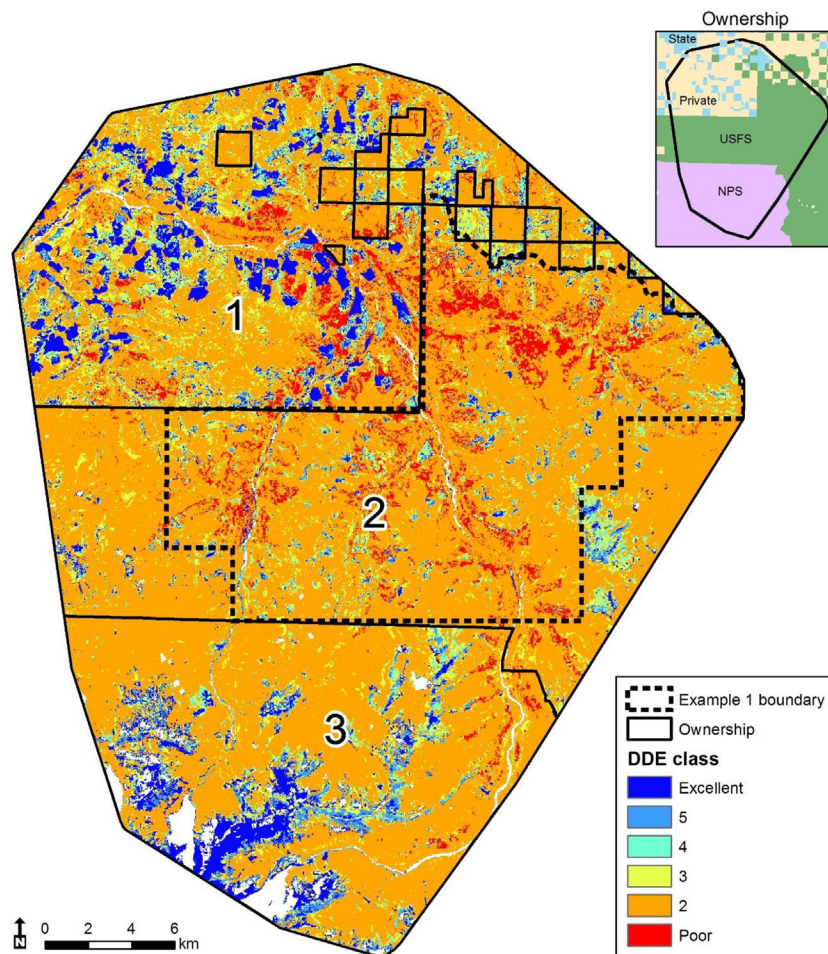


Figure 34. Six elk nutrition classes of dietary digestible energy (DDE) for example 2 mapped by 2010 land ownership, composed of private industrial forest (private, ownership 1), Mt. Baker-Snoqualmie and Wenatchee National Forests (USFS, ownership 2), and Mount Rainier National Park (NPS, ownership 3), Washington, USA. A small percentage of state lands was included in the private category because small tracts of state-owned lands were interspersed among large areas of private industrial forest. Boundaries of the example 1 area lie entirely within the national forest portion of the example 2 area, as outlined in dotted lines. Nutrition classes are estimated for conditions in 2010. Masked areas represent non-habitat (e.g., rock, water) and are displayed in white.

Table 14. Percent area by dietary digestible energy (DDE) class for the regional landscape for the current time period by the 3 major land ownerships discussed in example 2, and the predicted pregnancy rates and percent body fat of lactating female elk based on percent area in nutrition classes 3–6^a and 4–6^b, respectively. A small percentage of state lands was included in the private category because small tracts of state lands were interspersed among large areas of private industrial forest. We used year 2010 conditions to estimate DDE.

	DDE class ^c						Pregnancy rate (%)	Body fat (%)
	1	2	3	4	5	6		
Private	6.0	54.7	17.7	5.9	2.9	12.9	0.99	15
National forest	6.6	79.2	8.4	2.4	1.7	1.7	0.63	9
National park	0.9	70.7	10.1	2.5	5.6	10.2	0.94	14

^a Equation for predicting pregnancy rates of lactating female elk (Y), where $x = \% \text{ area with DDE} > 2.58 \text{ kcal/g}$ and $y = e^{(-1.709 + 0.157x)} / 1 + e^{(-1.709 + 0.157x)}$.
^b Equation for predicting percent body fat of lactating female elk (Y), where $x = \% \text{ area with DDE} > 2.75 \text{ kcal/g}$ and $y = 6.1 + 0.43x$. For landscapes with 0% area of DDE $> 2.75 \text{ kcal/g}$, percent body fat = 6.1%, which is the Y intercept of above equation. Predictions of body fat are capped at 15% when using this equation because of limitations in inference in making body fat predictions at higher levels.
^c The DDE values (kcal/g) for classes were 1 = < 2.40 ; 2 = $2.40\text{--}2.58$; 3 = $> 2.58\text{--}2.75$; 4 = $> 2.75\text{--}2.83$; 5 = $> 2.83\text{--}2.90$; 6 = > 2.90 .

pregnancy rates approaching 1.0 (Table 14). National forest lands, by contrast, had 14.2% of area in nutrition classes 3–6 and a predicted pregnancy rate of 0.63 (Table 14). Private industrial forest and Mount Rainier National Park also had large areas in nutrition classes 4–6; associated predictions of body fat of lactating females on these ownerships were 15% and 14%, respectively (Table 14). National forests had 5.8% of area in classes 4–6 and predicted body fat of 9% for lactating female elk (Table 14).

Areas of higher nutrition were associated with recent clearcut harvest on private industrial forest or high-elevation meadows within Mount Rainier National Park (Fig. 34). By contrast, national forest lands were dominated by canopy cover levels $> 70\%$ and associated low nutrition. This high canopy cover reflects the lack of active silviculture during the past 25 years on USFS lands, and lack of wildfire in wilderness and roadless areas over the same period (USDA Forest Service 2012a, b). However, if option 2 from example 1 is implemented on the national forest portion of example 2 (Fig. 30), the percent area in higher nutrition classes will increase substantially on USFS lands, as shown earlier (Fig. 31; Table 13). Moreover, a slightly larger increase in clearcutting area under option 2 would result in substantially higher elk performance, as discussed earlier.

Habitat-Use Predictions, Example 2

Elk use was predicted to be highest on private industrial forest, followed by Mount Rainier National Park (Fig. 35), as would be expected by the higher levels of nutrition on these land ownerships and limited open roads (Figs. 30 and 34). Only 14% of elk use was predicted to occur on national forest, in contrast to 49% and 37% of use predicted on private lands and Mount Rainier National Park (Fig. 35).

Although these patterns of elk use across ownerships were associated with like patterns in nutrition, the differences in habitat use across ownerships were magnified and diverged further by additional differences in road management (Fig. 30). Mount Rainer National Park had limited open roads. Private lands included a large network of 1,660 km of roads, but only 254 km of these roads were open to unrestricted motorized use by the public. By contrast, national forest lands had 843 km of roads with 666 km of roads open to public motorized use. The combination of higher nutrition and lack of open roads on private land, in contrast to the lower nutrition and a large network of open roads on national forests (Figs. 30 and 34), explains

predicted elk use being 3 times higher on private lands than on the adjacent national forests (Fig. 35). Similar differences in nutrition and open roads between Mount Rainier National Park and national forest lands explain the substantially higher predicted elk use in the Park.

Implementation of option 2 of example 1 on national forest lands would reduce differences in elk use across ownerships in example 2. Elk use increases from 13% beforehand (Fig. 35) to 15% afterward on national forest lands. This increase in elk use may seem biologically insignificant, but only a small percentage (1–2%) of the national forest land under example 1 is being treated to achieve this increase. Although predicted elk use would remain higher on private industrial forest and NPS lands, the implementation of option 2 under example 1 illustrates how changes in elk use, and associated distributions of elk, are possible to achieve through coordinated management across ownerships. Obviously, implementing nutritional improvements and road closures over a substantially larger percentage of the national forest lands would increase elk use far more than occurred in example 1, and could be implemented to a degree that shifts in elk distribution to public lands may start to occur.

DISCUSSION

Modeling Applications

The 2 examples illustrate key management uses and benefits of the models, which can be applied to regional and local landscapes to evaluate regional and local conditions. The models also can be applied within and across land ownerships to evaluate current conditions and management options that consider the dominant land uses in Westside landscapes. Results can be used as the basis for setting elk management objectives on public or private lands and for designing management prescriptions to meet the objectives.

Use of the nutrition model in example 1 demonstrated how different types and areas of silvicultural treatments can be evaluated for nutritional improvements, and in turn, how pregnancy rates and body fat of lactating female elk are affected. Regeneration harvest such as clearcutting, for example, resulted in a much stronger nutritional response compared to commercial thinning. That is, a reduction in canopy cover to 0%, *via* clearcutting, or to $< 10\%$ via shelterwood or seed-tree regeneration harvest, results in a substantially higher increase in DDE per unit area treated than does commercial thinning. Regeneration harvest shifts DDE to the highest nutrition class (class 6; Table 13), which has the greatest

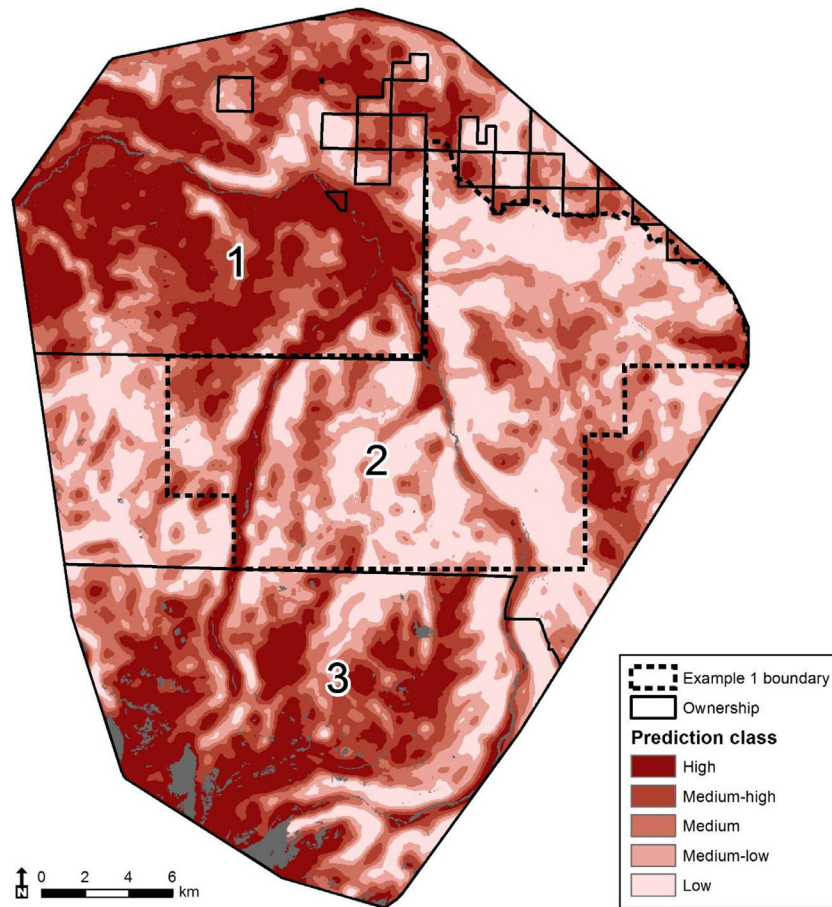


Figure 35. Relative probability of elk use for example 2 mapped by 2010 land ownership, composed of private industrial forest (ownership 1), Mt. Baker-Snoqualmie and Wenatchee National Forests (ownership 2), and Mount Rainier National Park (ownership 3), Washington, USA. A small percentage of state lands was included in the private category because small tracts of state-owned lands were interspersed among large areas of private industrial forest. Example 1 area lies within the national forest portion of the example 2 area, as outlined by dotted lines. Masked areas represent non-habitat (e.g., rock, water) and are displayed in gray.

benefit to pregnancy rates and body fat. Commercial thinning or other limited-entry silvicultural practices associated with a moderate reduction in canopy cover (e.g., to 40%) do not shift DDE to the highest nutrition class, and thus have more limited benefits to nutrition and animal performance (e.g., Table 12). However, the nutritional and animal performance benefits of any silvicultural practices that reduce canopy cover are clear, thus demonstrating the benefits of limited-entry silviculture such as commercial or pre-commercial thinning.

Habitat-use modeling in example 1 further demonstrated the need to consider all covariates that affect elk use. An increase in open roads under option 3 offset some of the benefits of increased nutrition, with a reduction in elk use under this option compared to options 1 and 2, despite a substantial increase in nutrition. The patch size of forage enhancements was small, which decreased the distance to cover-forage edges and increased elk use, as reflected by the distance to cover-forage edge covariate. In addition, forage enhancements occurred on gentle slopes, further increasing habitat use based on the slope covariate. Thus, all non-nutrition covariates in the habitat-use model contributed to increased use of the areas of improved nutrition. These results demonstrated how each covariate in the habitat-use model can be managed strategically, in combination, to achieve objectives for elk nutrition, habitat use, performance, and distribution. Results

further demonstrate the need to integrate management of all covariates in the habitat-use model if the benefits of increased nutrition are to be realized.

Example 2 demonstrated how a range of management options could be proposed to evaluate the degree to which elk distributions could be shifted to public lands through improved management of nutrition, roads, and arrangement of cover and forage areas, and in context of elk use of slope. If, for example, the objective was to triple elk use on national forest lands in the example 2 landscape, different combinations of silvicultural prescriptions and access management could be identified, mapped, and the models applied to identify which management approaches would meet objectives. Patch size of silvicultural treatments could be designed to further increase use based on distance to cover-forage edges. Silvicultural treatments placed on gentle slopes would further increase elk use of the areas of improved nutrition based on the slope covariate.

Differences in predicted elk use across land ownerships thus provide a foundation to design management strategies and activities to achieve objectives for elk nutrition, habitat use, distribution, and performance. Results can be used for coordinated landscape planning for elk across ownerships, and for consideration of conditions in adjacent ownerships as context for a given land owner's strategy for elk management.

These results have implications for managing elk distributions not only within these landscapes, but in relation to adjacent land ownerships (see Example 2). The substantial increase in habitat use is likely to maintain distribution of elk in the local landscapes, and has potential to shift some of the elk distribution to these areas of national forest from adjacent land ownerships (see Example 2).

The examples also illustrate how the models might be used to address the growing problem of elk shifting their summer distributions from higher-elevation forests to lower-elevation agricultural and urban areas (Thompson and Henderson 1998, Starr 2013). These shifts have been associated with elk finding refuge areas in agricultural and urban areas where they are not hunted, often resulting in long-term, year-round residence (Walter et al. 2011, Starr 2013). Simultaneous with these distributional changes has been the long-term decline in abundance of early-seral forest habitat on public lands in the Westside region (see summary by Wisdom et al. 2018a), which may motivate or accelerate landscape shifts by elk to lower-elevation agricultural and urban areas (Starr 2013).

Habitat Modeling for Elk

The Westside nutrition and habitat-use models performed well in predicting elk nutrition, habitat use, distribution, and performance under current conditions. Future sources of uncertainty, however, have the potential to reduce accuracy and utility of the models for management. Rowland et al. (2018) mention future sources of uncertainty that might affect model predictions, which include climate change; associated changes in forest insect dynamics; increased frequency, area, and intensity of wildfires; and changing density and composition of predators and their management. Additional sources of uncertainty include the future role of private forest owners in sustaining areas of high nutrition; the continued trend to further limit or eliminate hunting on private lands, leading to more refuge areas; and increased human activities on public lands, including poaching, that are facilitated by a large network of roads open to motorized access. Future research can address these uncertainties as environmental change continues in the Westside region, and models are modified and adapted to maintain their utility for management.

Despite these future sources of uncertainty, use of the models under current conditions is strongly supported by results from the modeling analyses. Our approach to modeling nutrition and habitat use for elk may provide a useful framework for research and management of wildlife species with coarse-scale habitat requirements. Voluminous but highly disparate data sets on animal use at landscape scales are now commonly available with the advent of GPS and satellite-based telemetry and remotely sensed vegetation parameters. These data can now be assimilated and analyzed for habitat modeling across large areas of a species' range with the use of ubiquitous, coarse-scale GIS data to estimate covariates, and the use of GPS-based telemetry data to estimate animal use. Unfortunately, extensive data sets on animal performance are typically limited for most areas and are more difficult and expensive to acquire.

Taking advantage of these large and disparate data sources for habitat modeling demands more investment in the design of

modeling approaches, especially for management uses. New methods of meta-analysis and meta-replication can now be used to develop and validate habitat models across a vast inference space, such as an ecoregion or biome. Our work was based on integration of a wide range of large and disparate data sets to gain knowledge of a species' habitat needs and the evaluation of those needs, at scales meaningful to the species and to management. Use of such methods, and their further improvement with future modeling work, will continue to advance the ecology and management of wildlife species like elk.

MANAGEMENT IMPLICATIONS

Diverse Land Ownerships and Objectives

Elk are typically not the primary focus of management on public or private lands in the Westside region. Public forests throughout the region are under the direction of the Northwest Forest Plan (USDA Forest Service and USDI Bureau of Land Management 1994a, b), which focuses on sustaining and increasing the abundance of late-seral forest stages for recovery of late-seral wildlife species such as the northern spotted owl and marbled murrelet (*Brachyramphus marmoratus*). During the past 25 years since the Northwest Forest Plan was enacted, the abundance of early-seral vegetation has declined substantially, and now composes a small and declining percentage of public forests in the Westside region (Weisburg and Swanson 2003, Cook et al. 2018). This change contrasts with the historical abundance of early-seral vegetation that occupied up to 35% of forest area in the region (Weisburg and Swanson 2003). The current paucity of early-seral vegetation on public forests has prompted litigation by Native American tribes to prompt restoration of these vegetation types for hunted species such as elk, which are a key subsistence food on public lands ceded for tribal harvest in the region (USDA Forest Service 2001a, b).

Industrial forest owners, by contrast, typically manage Westside lands for intensive timber harvest, even-aged management, and short rotation lengths. This combination produces large areas of early-seral vegetation with high elk nutrition (Cook et al. 2016, 2018; Geary et al. 2017). However, the degree to which intensive timber management can sustain high elk nutrition also depends on the reforestation methods used to establish commercial conifers after timber harvest (Witmer et al. 1985). Efforts to truncate early-seral forest development and duration to meet goals for industrial forest production may further diminish future maintenance of early-seral conditions (Swanson et al. 2011, 2014). Despite this trend, the large amount of area subjected to clearcutting under short timber harvest rotations (e.g., 30–40 years) on private industrial forest (Geary et al. 2017), and similar rotations on many tribal lands (Vales et al. 2017), are likely to continue to produce substantial areas of high nutrition. Elk use of areas of higher nutrition is further affected by the shape of openings (distance to cover-forage edge), management of roads (distance to roads open to public motorized use), and slope (percent slope), per our habitat-use model.

The challenge of how to address poor and marginal nutritional conditions that dominate public lands throughout the region represents a major dilemma for elk management. Public and private forests occupy an equally large percentage of the Westside

region (~44% each; Wisdom et al. 2018a); both ownerships thus have a major effect on elk nutrition and habitat use. Under current conditions and those likely to be maintained on public forests under the Northwest Forest Plan, only small areas of public land will meet the summer nutritional requirements of lactating female elk (Cook et al. 2018). This habitat void is likely to result in a population distribution of elk that is largely concentrated on private forests, agricultural lands, and areas closed to hunting near or within smaller towns or areas of rural-urban interface. An elk distribution largely concentrated on private lands will severely limit opportunities for hunting and viewing of elk on public lands, as well as eliminate or substantially curtail traditional tribal hunting on ceded public lands.

To achieve desired objectives for elk nutrition, habitat use, distribution, and performance, within and across land ownerships, explicit management prescriptions for elk must be integrated with other prescriptions for multiple-use management. Research is needed that evaluates the trade-offs and spatial and temporal optimization of different landscape management objectives for different sets of species and habitats, including elk and other early-seral versus late-seral species. The Northwest Forest Plan is currently under review for renewal, following the time requirements for revision established when it was implemented (USDA Forest Service and USDI Bureau of Land Management 1994a, b). The historically low abundance of early-seral vegetation on public forests in the Westside region will likely be part of the public's discussion of possible refinements to the Northwest Forest Plan; this discussion is further justified by the large number of early-seral wildlife species in the Westside region (Hagar 2007) and strong tribal interest in the topic (USDA Forest Service 2001a, b).

Poor nutrition and extensive areas of open roads are obviously 2 key factors that pose challenges to achieving desired elk habitat use, population distributions, and associated animal performance across ownerships at landscape scales in the Westside region (Cook et al. 2018, Rowland et al. 2018). These challenges often warrant evaluation and management of elk conditions across multiple land ownerships to identify and maximize opportunities for maintaining elk distributions in desired areas for recreation objectives. New agreements between public and private forest managers could be considered to more fully coordinate the management of nutrition and roads in a manner that provides support for increased elk distribution within and near public lands; or to provide additional public recreational opportunities for elk viewing and hunting on private lands as a mitigation for lack of early-seral vegetation being sustained on public lands. Such coordination is now possible in using the spatially explicit nutrition and habitat-use models. Roads open to public motorized use are common on public lands and have the potential to substantially reduce elk use of areas of higher nutrition and shift or maintain distributions away from public lands (per example 2).

Stakeholder Engagement in the Modeling Process and Applications

Effective development and management applications of the nutrition and habitat-use models were facilitated by long-term engagement of key stakeholders in the Westside region. Ideas for the modeling came from hunting conservation organizations,

who organized meetings with public land managers and scientists in the region to discuss elk management issues and associated modeling needs. These discussions led to a federal advisory group's formal recommendations to the Secretaries of Interior and Agriculture to begin a new round of elk habitat modeling in the Westside region (Wisdom et al. 2018a). These recommendations prompted federal agency leaders to recruit scientists to lead the modeling process.

Stakeholder engagement continued and grew as part of the formal modeling process. The group of scientists recruited to conduct the modeling was affiliated with a diverse set of tribal, state, federal, university, and private partners who had a direct stake in elk research and management. No interested partners were excluded. Data used for modeling were provided by 5 Native American tribes, a state wildlife agency (Washington Department of Fish and Wildlife), the timber industry (National Council for Air and Stream Improvement and associated timber companies), and a university (Oregon State University; Table 7). Funding and staffing support for the work also was diverse and substantial, including over 20 different tribal, state, federal, private, and university sources.

The diversity of science and management engagement in the modeling process was further enhanced by a series of meetings and 2 formal workshops conducted by the scientists during model development (<https://www.fs.fed.us/pnw/research/elk/westside/index.shtml>). Meetings and workshops were used to share modeling ideas and preliminary results, and obtain feedback from stakeholders about how the models could be improved for management applications. The process was transparent and continuous throughout, allowing the models to be improved iteratively through stakeholder input. In addition, the draft models were beta-tested by a large group of tribal, state, and federal biologists to further evaluate and improve management utility. Results from these tests helped refine and finalize the models for application in practical ways at spatial and temporal scales of interest to managers. Finally, the draft models underwent early and rigorous peer review before manuscript submission for publication to address the scientific merits and rigor of the work and facilitate timely management uses before formal publication.

In response to these activities, the USFS and USDI Bureau of Land Management formally endorsed the models as official corporate tools to evaluate and manage elk nutrition and habitat use on federal lands in the Westside region. The endorsement was outlined in a joint letter from both agencies dated 21 February 2013 directed to their land managers and biologists. This process and support led to early adoption and effective use of the models on federal (e.g., Doerr 2016) and tribal lands (Vales et al. 2017). The effectiveness of continuous and transparent stakeholder engagement in elk modeling illustrates the benefits of such a process in facilitating management uses of wildlife habitat models as a partnership between scientists and stakeholders.

Adaptive Management Partnerships

Given the significant ecological and economic benefits of elk, their cultural connection with Native American Tribes, and the socio-political status of the species, we anticipate increased focus

on restoration of early-seral vegetation to benefit elk and other early-seral species in the Westside region (Swanson et al. 2014). Adaptive management, as originally defined by Walters (1986), is a key part of the Northwest Forest Plan (USDA Forest Service and USDI Bureau of Land Management 1994*a, b*); its renewal may provide additional opportunities to design, implement, and test concepts of early-seral management for associated wildlife (Hagar 2007).

Use of adaptive management to enhance elk habitat would be particularly effective if integrated with state wildlife agency goals for elk within and across state wildlife management units. The Washington Department of Fish and Wildlife and the Oregon Department of Fish and Wildlife have established elk population goals for their wildlife management units (Washington Department of Fish and Wildlife 2002*a, b, c*, 2004, 2008, 2013; Oregon Department of Fish and Wildlife 2003, 2005), but detailed objectives have not been established for managing elk distributions and performance within and across land ownerships within the units. These additional objectives would provide essential context for effective management of nutrition and habitat use with model applications. Adaptive management approaches for elk are further complicated by management of roads open to public motorized use, which often is a polarizing issue among many public groups (Stern et al. 2009). Resolving the road management issue to meet elk objectives will require close coordination and planning between elk managers and diverse public interests.

Despite these challenges, our validated models provide a strong scientific basis for management of elk habitats and populations. All landowners now have opportunities to use the models to coordinate management within and across ownerships to achieve goals for elk distribution and performance. Development and use of habitat models like those described here could provide similar opportunities for management in other areas of elk range in North America, where elk constitute a major economic and social resource, and where debate and conflict regarding management of population distributions and performance are currently unresolved (Wisdom and Cook 2000).

SUMMARY

Distributions of elk in western North America are shifting from public to private lands, leading to foregone recreational opportunities for the public and conflicts with private landowners. Tools that predict nutritional resources and distributions of elk across large landscapes can benefit management of elk across land ownerships. We developed and validated regional models of elk nutrition and habitat use for application in western Oregon and Washington, USA (Westside).

We used data collected during foraging experiments with captive female elk and field measurements of site characteristics from 349 macroplots in 3 Westside study areas to develop the nutrition model. The habitat-use model incorporated 13 unique telemetry data sets of female elk from multiple sources and 7 study areas.

- Predictions of dietary digestible energy (DDE) varied widely among predominant potential natural vegetation (PNV) zones, with the preponderance of Westside landscapes failing to meet basic requirements of DDE for lactating female elk. Generally,

highest DDE levels occurred in zones occupying higher elevations and in early-seral communities. Lowest DDE levels occurred at lower elevations and in closed-canopy forests.

- We found strong regional gradients in DDE north to south (higher to lower) in the Cascades and east to west from the Cascades to the Coast Range. Autumn body fat and pregnancy rates of wild lactating elk varied similarly across the region.
- We evaluated the nutrition model by comparing predicted DDE levels to higher order responses of elk, including resource selection, autumn body fat, and pregnancy rates. Elk strongly selected for areas providing relatively high DDE. Mean autumn body fat and pregnancy rates of lactating elk in 9 Westside elk populations were positively correlated to percent area providing DDE levels that met or exceeded basic requirement (>2.58 kcal/g DDE).
- Disturbance regime and forest succession also were closely linked to DDE, suggesting that habitat management, such as thinning, on Westside summer ranges can significantly influence elk distributions and productivity (e.g., pregnancy rates).
- The nutrition model demonstrated that data on foraging dynamics and ungulate nutrition collected at fine scales can reliably index performance of elk populations at broad scales in the Westside region.
- We used a hierarchical approach to develop the habitat-use model by considering individual study areas as replicates to predict relative probability of use by elk across the Westside.
- The regional habitat-use model best supported by the empirical data had 4 covariates: DDE, distance to nearest road open to motorized use by the public, distance to cover-forage edge, and slope. Predicted elk use was greater in areas with higher DDE, farther from open roads, closer to cover-forage edges, and gentler slopes.
- Our regional habitat-use model performed well using independent telemetry data, with high correlation between predicted and observed use by elk in most validation sites.
- We demonstrated the management utility of the nutrition and habitat-use models through 2 examples in western Washington, comparing nutritional conditions and predicted use by elk across land ownerships and scales in response to several management scenarios. Results indicated that relatively small-scale improvements in habitat (e.g., road closures, clearcuts, or thinning) can lead to biologically meaningful increases in animal performance and greater relative probability of use by elk.
- We conducted a meta-analysis of disparate data sets on elk habitat use synthesized from multiple areas and years for model selection and validation. We found consistent patterns of habitat use across the populations sampled. This replicable approach can be used for other wildlife species to better understand regional patterns of use and thus improve management efficiency and consistency. We further demonstrated that mechanistic processes of nutrition and human disturbance in our study areas can be successfully modeled with coarse spatial data to accurately estimate elk use at regional scales.
- Our models and approaches can inform management (e.g., manipulating landscapes through actions such as silviculture and road management) to improve elk nutrition, habitat use, distributions, and performance.

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SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this monograph at the publisher's website.

Supporting Information

Rowland, M. M., M. J. Wisdom, R. M. Nielson, J. G. Cook, R. C. Cook, B. K. Johnson, P. K. Coe, J. M. Hafer, B. J. Naylor, D. J. Vales, R. G. Anthony, E. K. Cole, C. D. Danilson, R. W. Davis, F. Geyer, S. Harris, L. L. Irwin, R. McCoy, M. D. Pope, K. Sager-Fradkin, and M. Vavra. 2018. Modeling elk nutrition and habitat use in western Oregon and Washington. *Wildlife Monographs* 199:1-69.

APPENDIX A. DESCRIPTION OF HABITAT-USE MODELING AREAS FOR WESTSIDE ELK HABITAT-USE MODELS

To develop and validate habitat-use models for elk, we analyzed environmental variables and elk telemetry data from female elk for 13 modeling areas and associated data sets, nested within 7 Westside study areas (Table 1). These sites ranged from Nooksack in northern Washington to Coquille in southwestern Oregon (Fig. 17; Tables 1, A1). We defined a study area as a distinct geographic area within which ≥ 1 data sets were collected, and a data set as a specific type of empirical data (e.g., nutrition, habitat use) collected within a given study area and time period used as a unit of replication to develop or validate nutrition or habitat-use models (Table 1). We analyzed telemetry data from 5 data sets for model development: 1) Green-Cedar 2008; 2) Pysht 2009; 3) White River 2004; 4) White River 2005; and 5) White River 2007. We acquired telemetry data from 8 additional areas for use in model validation: 6) Coquille North 1991–1992; 7) Coquille North 1993–1994; 8) Coquille South 1991–1992; 9) Coquille South 1993–1994; 10) Green-Cedar 2006–2007, 2009; 11) Makah 2000–2003; 12) Nooksack 2008–2009; and 13) Quileute 2006–2008. Cook et al. (2016) describe study areas used in grazing trials for captive elk that provided data for developing the Westside nutrition model.

Habitat-use modeling areas were characterized by temperate, coniferous rainforests that received high levels of precipitation fall-spring but experienced predictable drought during summer (Franklin and Dyrness 1988). Dominant ($>50\%$ of existing vegetation in ≥ 1 modeling area) forest types included Pacific silver fir, red alder, Port Orford cedar (*Chamaecyparis lawsoniana*), Douglas-fir, western hemlock, western red cedar, and mountain hemlock. Douglas-fir-western hemlock was the most abundant existing vegetation type in most modeling areas and the Westside region overall (Franklin and Dyrness 1988).

Habitat-Use Model Development Areas and Data Sets

Green-Cedar 2008.—The Green-Cedar 2008 data set was associated with the Green River study area in the Cascade Range of western Washington, south of North Bend and east of Lake Washington. The area was drained by both the Green and Cedar Rivers, with the larger Green River watershed located south of the Cedar River watershed. Topography was gentle to moderately steep, and elevations moderate to high compared to other modeling areas (Table A1). Forest composition was dominated by western hemlock-western red cedar. Tree canopy cover was the greatest among all modeling areas ($\bar{x} = 79\%$), and density of roads open to public motorized access (0.20 km/km^2) was the second-lowest of any modeling area (Table A1). The Cedar River portion of the modeling area was largely owned by the City of Seattle and managed to supply water for the city. The Green River portion was owned by several landowners, but access was controlled and managed by Tacoma Water to supply water to the City of Tacoma. To protect drinking water, both watersheds were closed to public entry. To maintain water quality in

the Cedar River drainage, timber harvest has been minimal compared to other modeling areas, resulting in the relatively high canopy cover. By contrast, timber harvest in the Green River watershed has created a stand age-canopy cover mosaic more diverse than that in Cedar River.

This modeling area fell within 2 Washington Department of Fish and Wildlife Game Management Units (GMUs): Green River and Cedar River. Green River elk numbers declined during the 1990s and early 2000s, but that trend reversed and numbers grew rapidly during the study period (Washington Department of Fish and Wildlife 2013). Elk herds had recovered to about 60% of their historical highs (D. Vales, Muckleshoot Indian Tribe, personal communication). Introductions of Rocky Mountain elk led to colonization in the Cedar River drainage, and the herd grew rapidly (growth rate = 0.13) from 1970 to 1980, stabilizing later in the 1980s (Paige 1988). However, elk numbers in this unit have declined dramatically, even in the absence of hunting, and were estimated at 25% of their 1989 levels (Spencer 2002). Paige (1988) provided additional description of the Green and Cedar River areas.

Pysht 2009.—The Pysht study area was in the Olympic Mountains of northwest Washington, immediately south of the Strait of Juan de Fuca near Clallam Bay. Elevation was lowest among all modeling areas, ranging from sea level to 358 m. Topography was undulating, and slope was gentle to moderate ($\bar{x}$ = 16%). The dominant vegetation type was western hemlock-red alder. Density of roads open to public access (0.23 km/km²) was the third-lowest among modeling areas; only the 2 Green-Cedar data sets had lower values (Table A1). Over 90% of lands were privately owned and were managed for intensive timber production. Overstory canopy cover was low ($\bar{x}$ = 58%; Table A1), likely reflecting the dominant land use. The Pysht study area was within the Pysht GMU, where population size and productivity of Roosevelt elk have remained stationary over the past decade (K. Sager-Fradkin, Lower Elwha Klallam Tribe, personal communication). An estimated 100 elk were in this GMU in 2000, but the population objective was 300 during the study years (Washington Department of Fish and Wildlife 2004). Female-calf and male-female ratios have been higher on the privately owned Pysht Tree Farm than those on surrounding areas. The landowners maintained tight control over elk harvest, with only a few males removed annually from the tree farm (K. Sager-Fradkin, Lower Elwha Klallam Tribe, personal communication).

White River.—Three habitat-use modeling areas (White River 2004, 2005, and 2007) were near Enumclaw in the Central Cascades of Washington, equidistant between the Canada-United States border to the north and the Oregon-Washington border to the south. The areas were drained by the White River, West Fork White River, and Greenwater River. Elevations were the highest among all habitat-use modeling areas (Table A1), and the White River 2005 and 2007 areas included a portion of Mount Rainier at the highest elevations. Topography was mostly moderate to steep, and the White River 2004 area had one of the highest mean slope values among modeling areas (41%). Vegetation was dominated by Douglas-fir and western hemlock. Highest elevations supported large areas of alpine meadows in Mount Rainier National Park. Overstory canopy cover was intermediate among modeling areas ($\bar{x}$ = 69% to 73%). Ownership was 70% federal (primarily Forest Service) and 30% private timberlands in White River 2004, but 41% federal, 57% private, and 2% state lands in White River 2005 and 2007.

The 3 modeling areas were within Mount Rainier National Park and the White River GMU; the northernmost portion of White River 2007 also intersected the Green River GMU, described above. Most elk in the White River unit summered in the mountain hemlock zone within Mount Rainier National Park (Spencer 2002). Elk numbers here reached their peak in the early 1990s but declined sharply until early 2001 when they reached a low of about 30% of the

historical high (Spencer 2002). Numbers then rapidly rebounded and were at about 75% of the historical high during the study (D. Vales, Muckleshoot Indian Tribe, personal communication).

Habitat-use Model Validation Areas and Data Sets

Coquille.—Four validation data sets were from the Coquille study area: Coquille South 1991–1992, Coquille South 1993–1994, Coquille North 1991–1992, and Coquille North 1993–1994. All but 1 radio-collared elk used in our analyses remained on the same side of the East Fork of the Coquille River on which it was collared. Thus, we considered elk collared north of the river independent of those to the south. Moreover, the BLM implemented road closures in late 1992 to evaluate effects of vehicle access on elk movements, habitat use, and survival (Cole et al. 1997, 2004). Therefore we created separate data sets and associated modeling areas for elk in 1993–1994 because of their exposure to different levels of human disturbance than the 2 years prior.

The Coquille model validation areas were in the Coos Bay District of the BLM in the Southern Oregon Coast Range, about 30 km southeast of Coos Bay. This area was drained by the East and Middle Forks of the Coquille River. Elevations were low, ranging from 74 m along streams to 918 m, and terrain was the steepest among all modeling areas (Table A1). Until the late 1970s vegetation was primarily late-successional Douglas-fir and western hemlock. Intensive forest management resulted in a mosaic of clearcuts, Douglas-fir plantations and some old-growth stands during the years in which telemetry data were collected. Understory vegetation was sparse in plantations but denser in naturally regenerated stands and older forests (Cole et al. 1997). Open road density exceeded that of all other modeling areas, and was especially high in Coquille South 1991–1992 ($\bar{x} = 2.28 \text{ km/km}^2$) prior to road closures (Table A1). Total road density was also exceptionally high during the study years (6.04 km/km^2 ; Cole et al. 2004). Ownership was predominately federal, ranging from 43% in Coquille South 1993–1994 to 75% in Coquille North 1993–1994. Here, BLM lands created a checkerboard pattern intermixed with private lands, which ranged from 25% in Coquille North 1993–1994 to 53% in Coquille South 1993–1994. Private lands were managed primarily for commercial timber production (Cole et al. 1997). Canopy cover ranged from 61% to 70% and was lower on the south side of the river, where timber harvest was more common.

All 4 Coquille modeling areas were within Oregon Department of Fish and Wildlife Tioga Wildlife Management Unit. Elk numbers in this unit in 2004, the latest year for which estimates were available, were above management objective (9,050, with an objective of 8,000; Oregon Department of Fish and Wildlife 2005). Productivity, measured by calves per 100 cows, was typical for Roosevelt elk in western Oregon (3-yr average = 32 in 2004; Oregon Department of Fish and Wildlife 2005). Cole et al. (1997, 2004) provided additional details about the Coquille area.

Green-Cedar 2006, 2007, 2009.—Environmental conditions and elk populations in this validation modeling area, located in the Cascades of western Washington, closely resembled those for Green-Cedar 2008 described previously (Table A1). This validation modeling area was also located in the Green River and Cedar River GMUs, and was the largest modeling area used in our analyses (53,630 ha; Table A1).

Makah 2000–2003.—The Makah study area was located in the Olympic Mountains of northwest Washington, adjacent to both the Pacific Ocean and the Strait of Juan de Fuca. It spanned the southeast corner of the Makah Indian Reservation and areas immediately south and

east of the Reservation. A small portion of Olympic National Park intersected the southwestern portion of the study area. The area was drained by the Hoko, Sekiu, Sooes, and Big Rivers, and topography was gentle to moderate (Table A1). Elevation was low, ranging from sea level to 650 m, and mean canopy cover was 75% (Table A1). Dominant overstory vegetation was western hemlock-Sitka spruce (*Picea sitchensis*); understory vegetation was dominated by salal (*Gaultheria shallon*), huckleberry (*Vaccinium* spp.), blackberry (*Rubus* spp.), and red elderberry (*Sambucus racemosa*; Hutchins 2006). Road density was low (Table A1), and most (82%) of the area was in private lands managed for intensive timber production (Hutchins 2006), along with smaller areas of tribal and state lands. The Makah site encompassed nearly all of the Hoko GMU and the western portion of the Dickey GMU, units that are managed as part of the larger Olympic Elk Herd (Washington Department of Fish and Wildlife 2004). In the early to mid-1990s the elk population was in decline because of excessive hunting of cow elk; however, populations have increased significantly over the past 15 years with changes in hunting regulations and appeared to have stabilized (R. McCoy, Makah Forestry, personal communication). Hutchins (2006), Storlie (2006), and Boyd (2009) provided additional details about the study area and elk populations.

Nooksack 2008–2009.—The Nooksack validation modeling area was within the western foothills of the North Cascades in Washington, immediately south of the United States-Canada border and east of Sedro-Woolley. The core area was drained by the South Fork Nooksack River. Elevations spanned the widest altitudinal range of any data set, from 30 m to 1,952 m, and slopes were moderate to steep (Table A1). Forest vegetation was dominated by Douglas-fir-western hemlock; western hemlock was the primary timber production type in this area (Bender et al. 2006). Density of roads open to public motorized access was relatively low ($\bar{x} = 0.49$ km/km²). The modeling area was comprised of primarily private (60%) and state (32%) lands managed for intensive timber production.

Nearly all of the area was within the Nooksack GMU, although the southern boundary intersected the Sauk GMU; these units were managed as part of the larger North Cascade (Nooksack) Elk Herd, the smallest of the 10 elk herds managed by Washington Department of Fish and Wildlife (Davison 2002). Elk damage to agricultural lands along the Skagit River Valley was a contentious issue in this area (Davison 2002). Elk numbers declined substantially from about 1,700 elk in the early 1980s to 425 by the early 2000s (Davison 2002). Despite habitat improvements and cessation of all non-Tribal hunting, populations did not rebound (Bender et al. 2006). These conditions precipitated a translocation of 98 elk from Mount St. Helens (2003–2005; McCorquodale et al. 2013). Subsequently total population size of elk has increased substantially, and distribution has expanded (McCorquodale et al. 2013). See Bender et al. (2006) and McCorquodale et al. (2013) for additional details about the modeling area and elk populations.

Quileute 2006–2008.—Quileute, located in the Dickey River watershed on the Olympic Peninsula near La Push, Washington, was in the Forks study area and was the smallest of our 13 modeling areas (2,701 ha; Table A1). Elevation was low, ranging from sea level to 138 m, and topography mostly flat (Table A1). Dominant vegetation was western hemlock-red alder. Private lands were most common (66%) in this area, followed by state-managed holdings (22%); the remaining land was federal and fell within Olympic National Park. The modeling area was within the Dickey GMU, where body fat and condition scores indicated nutritional limitations to nutritional condition in the early 2000s (Washington Department of Fish and Wildlife 2004, Cook et al. 2013). The elk population in this GMU was at 80% of Washington Department of

Fish and Wildlife management objectives in 2000 (Washington Department of Fish and Wildlife 2004). In the early to mid-1990s elk numbers in this area declined significantly, primarily because of excessive hunting, but have since recovered and remained relatively stable (F. Geyer, Quileute Tribe, personal communication).

Table A1. Characteristics of data sets used to model elk habitat use in western Oregon and Washington, USA, organized by study area and model use: model development and model validation.

Study area	Data set ^a	Latitude/ longitude	Area (ha)	Potential natural vegetation ^b	Slope (%; mean)	Elevation (m)	Canopy cover (%; mean) ^c	Open road density (km/km ²) ^d
Model development								
Green River	GC08	47.368070/ -121.777152	30,671	TSHE	28.92	132–1,446	75.9	0.20 (0–7.53)
Pysht	PY09	48.193715/ -124.180459	7,135	TSHE	15.99	0–358	57.9	0.23 (0–3.11)
White River	WR04	47.021605/ -121.670021	32,601	PSME	41.39	393–2,226	72.7	0.57 (0–7.90)
	WR05	47.064265/ -121.680993	15,431	PSME	34.73	478–2,185	69.3	0.31 (0–5.99)
	WR07	47.080591/ -121.669365	35,019	PSME	39.40	358–2,258	68.8	0.39 (0–7.91)
Model validation								
Coquille	CN9192	43.198896/ -123.828783	13,478	TSHE	47.15	130–841	69.6	1.89 (0–7.43)
	CN9394	43.207840/ -123.871210	11,695	TSHE	47.40	74–828	69.7	1.39 (0–7.43)
	CS9192	43.063013/ -123.863063	9,334	TSHE	35.74	198–918	62.5	2.28 (0–7.79)
	CS9394	43.065696/ -123.872537	9,148	TSHE	35.23	84–906	61.4	1.44 (0–8.55)
Green River	GC0609	47.338351/ -121.738389	53,630	TSHE	31.35	183–1,553	75.6	0.13 (0–7.53)
Makah	MK0003	48.221235/ -124.518507	47,196	PSME	24.11	0–650	75.0	0.33 (0–7.93)

Nooksack	NK0809	48.621289/ -121.994890	38,625	PSME	30.83	30–1,952	72.9	0.49 (0–9.34)
Forks	QU0608	47.937124/ -124.583950	2,701	TSME	8.16	1–138	73.6	1.23 (0–7.61)

^a Codes indicate study area and year: GC08 = Green-Cedar 2008; PY09 = Pysht 2009; WR04 = White River 2004; WR05 = White River 2005; WR07 = White River 2007; CN9192 = Coquille North 1991–1992; CN9394 = Coquille North 1993–1994; CS9192 = Coquille South 1991–1992; CS9394 = Coquille South 1993–1994; GC0609 = Green-Cedar 2006, 2007, 2009; MK0003 = Makah 2000–2003; NK0809 = Nooksack 2008–2009; QU0608 = Quileute 2006–2008.

^b Dominant potential natural vegetation within modeling area, where TSHE = western hemlock (*Tsuga heterophylla*) zone, PSME = Douglas-fir (*Pseudotsuga menziesii*) zone, and TSME = mountain hemlock (*Tsuga mertensiana*) zone.

^c Calculated as mean canopy cover for all 30-m × 30-m pixels within a 350-m radius sampling circle.

^d Calculated as mean density of roads open to motorized use by the public within a 350-m radius sampling circle. Numbers in parentheses represent the range of values for all 30-m × 30-m pixels in the modeling area.

APPENDIX B. DESCRIPTION AND DERIVATION OF COVARIATES FOR MODELING ELK NUTRITION AND HABITAT USE

We acquired data from diverse sources to develop a comprehensive suite of covariates to model elk nutritional conditions and habitat use across the Westside region (Tables B1, B2). Given the large area evaluated, we sought data sources that 1) were easily manipulated to derive covariates suitable for model development, 2) were readily available at no cost, 3) provided continuous (wall-to-wall) coverage across either the entire Westside region (nutrition model) or the 5 model development and 8 validation sites (habitat-use model), and 4) were credible based on literature review and consultation with species experts. Here we describe key data sources, temporal matching of data with modeling years, and derivation of some of the more complex covariates (other covariates are described in Table B2). Although we initially explored the full suite of covariates (Table B1), we did not fully derive all of them throughout each modeling area (e.g., if data were not widely available, such as traffic rates).

Data sources described here also provided the foundation for modeling applications and programs used to apply the models. The Westside nutrition and habitat use models are available for download as an ArcGIS toolbox, along with a user's guide describing the preparation of input layers and methods for summarizing model outputs (Rowland et al. 2013; <http://www.fs.fed.us/pnw/research/elk/toolbox/index.shtml>).

Primary Data Sources

Key spatial data sources for developing modeling covariates were 1) USFS, modeled PNV zones (<http://ecoshare.info/products/gis-data/>, accessed 20 Feb 2014); 2) Landscape Ecology, Modeling, Mapping, and Analysis (LEMMA) project, existing vegetation characteristics and landcover types <http://www.fsl.orst.edu/lemma/main.php?project=nwfp&id=studyAreas>, accessed 20 Feb 2014); 3) Bureau of Land Management Ground Transportation (GTRN) project, existing roads (<http://www.blm.gov/or/gis/data.php>, accessed 20 Feb 2014); and 4) United States Geological Survey, elevation (<http://ned.usgs.gov>, accessed 20 Feb 2014).

PNV zones.—Cook et al. (2018) developed nutrition equations for the 3 dominant PNV zones in the Westside region and subsequently combined these into 2 zones (western hemlock and Pacific silver fir-mountain hemlock) to model elk nutrition. For the remaining 12 PNV zones that occurred in the Westside, we either crosswalked them to 1 of these 2 zones or excluded them (i.e., masked them from further analysis). Excluded areas constituted a very minor portion of the modeling area (Table 5). The concept of potential natural vegetation has been used by ecologists since the 1950s, and the natural vegetation zones of Washington and Oregon described by Franklin and Dyrness (1988) are commonly used for research and management applications in the Westside region. The mapped PNV zones we used in our project were based on a suite of environmental predictors such as elevation, slope, aspect, precipitation, topography, and solar radiation.

Existing vegetation.—We derived several key vegetation-based covariates from LEMMA data (Table B2), commonly referred to as GNN (gradient nearest neighbor) because of the imputation method used to populate grid cells with data for much of the Pacific Northwest region (Ohmann and Gregory 2002, Pierce et al. 2009). All covariates used in mapping elk nutrition relied on this data source. The distance to edge covariate in the habitat-use model also used GNN, as did many vegetation covariates considered during model selection (Table B1).

We used the GNN species-size map to develop vegetation covariates for model development (November 2009 release) and model validation (March 2010 release). Both releases reflect conditions as of 2006. For modeling the Coquille validation areas (Appendix A), we used the 1996 GNN data product. We used the existing vegetation field (ecological system, ESLE_NAME; Comer et al. 2003) from GNN to identify areas of non-habitat (e.g., cliff and talus, open water; Table B3) and masked these pixels from analysis. Non-habitat totaled about 8% of the Westside region. Additional vegetation data obtained from GNN were canopy cover of live trees, stand height, number of vegetation layers, quadratic mean diameter, and tree density (all trees and hardwoods only; Table B2).

Accuracy of vegetation types and structural features estimated by GNN was typical of contemporary vegetation mapping efforts, especially at regional scales, and varied by vegetation attribute (Ohmann and Gregory 2002, Pierce et al. 2009). We relied extensively on 1 key GNN attribute, live tree overstory canopy cover (CANCOV), for nutrition modeling and to calculate distance to edge for the habitat-use model (Table B2). Estimates of live tree canopy cover from GNN had an average root mean square error of 0.98 and an average correlation coefficient of 0.72 ($n = 1998$) in relation to empirical field estimates used for validation.

Roads.—We explored several sources of digitized roads layers for creating human disturbance covariates. We found that the continuous coverage transportation vector layer (GTRN) provided by the BLM (USDI Bureau of Land Management 2015) had the greatest spatial accuracy and coverage in our modeling region. This dataset spanned ownerships and included nearly every road in our modeling area. Visual examination of GTRN roads overlaid with digital aerial photos showed a high level of agreement (>90%) with road locations. Where omission errors were observed, we digitized missing roads. We identified roads absent from the GTRN data using imagery from the appropriate year of elk data locations, from maps provided by local field offices, and with assistance from local resource experts who had knowledge of local road systems. We also corrected placement of road segments that were >50 m from actual locations based on imagery.

We created an open-closed attribute for roads to reflect whether they were open to the public for motorized use during modeling periods (i.e., Jun–Aug, and by appropriate modeling year). Sources of information for open-closed status were USFS, private timber companies, and county governments. We relied on personnel familiar with each our study areas to verify whether a road was accessible (e.g., designated open but access blocked because of overgrown vegetation, landslides, etc.). If roads were officially designated as closed, but known to be occasionally used by the public, we classified them as closed. We did not formally evaluate accuracy of the classification of road types (open or closed to motorized access). Instead, these classifications were carefully reviewed and refined by resource professionals with expert field knowledge of local road status and use.

U.S. Geological Survey elevation data. —Physical model covariates were based on elevation estimates from the National Elevation Dataset (1/3 arc-second resolution), with mapping errors of <1 m at 10-m vector resolution (Gesch et al. 2014). Elevation data were the most accurate of any in our modeling, and a wide variety of physical covariates in both nutrition and habitat-use modeling were derived from elevation (Tables B1, B2).

Temporal Matching of Data Layers

Because some data layers we acquired did not match the vintage of elk telemetry data, we modified the layers to match the timeframe of our modeling period when possible. When telemetry data spanned multiple years for a single data set, we selected imagery from the year in which most locations were obtained for adjustments of vegetation inputs. For data sets in which the tree canopy cover input layer (CANCOV from GNN) was generated before the modeling year, we either obtained timber harvest boundaries from local land managers or hand-digitized harvest boundaries by viewing 1- to 3-m true color aerial photography from the National Agriculture Imagery Program (https://www.fsa.usda.gov/Internet/FSA_File/naip_info_sheet_2013.pdf, accessed 20 Feb 2014) from the modeling year. We assigned all cells within harvested units the canopy cover value associated with the acquired boundaries or estimated through photointerpretation. For data sets where the existing canopy cover layer was generated after the year modeled, such as Coquille, we identified and digitized polygons that had been harvested between the modeling year and the year of the canopy layer by comparing the 2 sources of information. We created a 100-m buffer around each harvest boundary, excluding areas in the buffer that were obviously harvested in prior years. We then calculated mean canopy cover within each buffered area and applied that value to all cells within the associated harvest unit to reflect canopy cover values that likely existed during the year modeled. We also adjusted stand height and hardwood proportion values, used to derive cover-forage patches (height) and DDE (hardwoods), within harvest polygons. In clearcuts, we assigned a value of 0 for stand height and hardwood proportion. In thinned units, however, we applied the original stand height and hardwood values to the polygon.

Derivation of Cover-Forage Patches and Edges

To create distance to cover-forage edge, we first defined cover as any 30-m cell with ≥ 40 percent canopy cover and > 2 m stand height. To avoid creating a pixelated cover map, we identified cover patches as groups of at least 3×3 adjacent cover cells. We classified all remaining cells as non-cover, including isolated cover cells. We then defined forage patches as patches of at least 3×3 adjacent non-cover cells. We assigned a no data value (i.e., data not used in cover-forage calculations) to any remaining cells not satisfying the cover or forage patch criteria above. We then created a line shapefile to represent edges between cover and forage patches; from that line we created a distance grid (distance-to-edge grid; Table B2). We calculated summary statistics for key modeling covariates (Table B4).

Table B1. Covariates initially considered in development of nutrition and habitat-use models for elk in western Oregon and Washington, USA, organized by covariate category. Grid cell size was 30-m $\times$ 30-m for all covariates.

Category	Covariate ^a	Units	Description
Nutrition	Accepted biomass	kg/ha	Mean biomass of neutral or selected ^b forage species within circular sampling unit ^c
	DDE	kcal/g	Mean DDE within circular sampling unit
	MGE	kcal/g	Mean DDE of pixels with values ≥ 2.40 (i.e., marginal or better) within circular sampling unit
	% MGE	%	% of circular sampling unit with DDE values ≥ 2.40 (i.e., marginal or better)
	Distance to nearest MGE patch (2 patch sizes)	m	Distance from center pixel of circular sampling unit to nearest patch of at least 3×3 or 7×7 contiguous pixels with DDE ≥ 2.40
Human disturbance	Distance to nearest high traffic open road ^d	m	Distance from center pixel of circular sampling unit to nearest open road classified as high traffic use
	Distance to nearest low traffic open road	m	Distance from center pixel of circular sampling unit to nearest open road classified as low traffic use
	Distance to nearest closed road	m	Distance from center pixel of circular sampling unit to nearest closed road
	Distance to nearest open road ^d	m	Distance from center pixel of circular sampling unit to nearest road open to public motorized use
	Distance to nearest road, all types	m	Distance from center pixel of circular sampling unit to any road type, open or closed
	Distance to nearest open road or trail	m	Distance from center pixel of circular sampling unit to nearest road or ATV trail open to public motorized use
	Distance to nearest road or trail open to administrative motorized use only	m	Distance from center pixel of circular sampling unit to nearest road or ATV trail open for administrative use only
	Density of open roads and trails	km/km ²	Density of open roads and ATV trails within circular sampling unit
	Density of open roads	km/km ²	Density of open roads within circular sampling unit

Category	Covariate ^a	Units	Description
Vegetation	% canopy cover	%	Mean % canopy cover of live trees within circular sampling unit
	Dominant canopy cover class	category	Dominant category of canopy cover within circular sampling unit, using 5 categories of 20% canopy cover intervals (e.g., 0–20%, 20–40%)
	Distance to nearest forage patch	m	Distance from center pixel of circular sampling unit to nearest forage patch ^e
	Distance to nearest cover patch (3 patch sizes)	m	Distance from center pixel of circular sampling unit to nearest cover patch of at least 3 × 3, 7 × 7, or 33 × 33 pixels ^f
	Distance to cover-forage edge	m	Distance from center pixel of circular sampling unit to nearest edge between cover and forage patches
	Cover-forage ratio	%	Ratio of number of cover pixels to number of forage pixels within circular sampling unit
Physical	% slope (center)	%	Percent rise at center pixel of circular sampling unit
	% slope (mean)	%	Mean % slope within circular sampling unit
	% slope (median)	%	Median % slope within circular sampling unit
	Sine of aspect	NA	Sine of aspect at center pixel of circular sampling unit
	Cosine of aspect	NA	Cosine of aspect at center pixel of circular sampling unit
	Dominant slope category	category	Dominant of 3 categories of slope: flat or gentle (0–30%), moderate or steep (31–70%), very steep (>70%); assigned to circular sampling unit
	% area in flat or gentle slope	%	% pixels in flat or gentle slopes (0–30%) within circular sampling unit
	% area in moderate or steep slope	%	% pixels in moderate or steep slopes (31–70%) within circular sampling unit
	% area in very steep slope	%	% pixels in very steep slopes (>70%) within circular sampling unit
	Convexity ^g		Convexity at center pixel of circular sampling unit
	Curvature	1/100 of a z-unit	Curvature at the center pixel of circular sampling unit
	Mean solar radiation	WH/m ²	Mean solar radiation within circular sampling unit

Category	Covariate ^a	Units	Description
	Dominant landowner	category	Dominant landowner class among generalized landownerships within circular sampling unit

^a Abbreviations: ATV, all-terrain vehicle; DDE, dietary digestible energy (kcal/g); MGE, marginal, good, or excellent DDE (see Cook et al. 2004 for details); WH, watt hours.

^b Neutral species are forage species for which use by elk was approximately equal to availability; selected species are forage species with a positive Ivlev index. See Cook et al. (2016) for details.

^c 350-m radius circular sampling unit used to summarize covariate values for model development areas.

^d Open included any road or trail open to motorized use by the public.

^e Forage pixels were defined as those with <40% tree canopy cover and stand height ≤ 2 m; a forage patch was at least 3×3 contiguous forage pixels (see Appendix B text).

^f Cover pixels were defined as those with $\geq 40\%$ canopy cover and stand height > 2 m; a cover patch was at least 3×3 contiguous cover pixels (see Appendix B text).

^g Measure of the convex or concave nature of a site, estimated by evaluating differences in elevation between center pixel and adjacent pixels (see Johnson et al. 2000 for details).

Table B2. Methods in ArcGIS^a and data sources used to derive covariates for final habitat-use models for elk in western Oregon and Washington, USA, organized by model set. Grid cell size was 30 × 30 m for all covariates.

Model set	Covariate name ^b	Derivation	Data source
Nutrition	Accepted biomass	Create accepted biomass raster using several expressions in RASTER CALCULATOR tool; use FOCAL STATISTICS tool to calculate mean of accepted biomass raster within circular sampling unit ^c	GNN: CANCOV, TPH_GE_3, TPHH_GE_3 ^d ; U.S. Forest Service: PNV zone; equations in Table 6
	DDE	Create DDE raster using several expressions in RASTER CALCULATOR tool; use FOCAL STATISTICS tool to calculate mean of DDE raster within circular sampling unit	Equations in Table 4
	MGE	Extract DDE pixels ≥2.40 (marginal or better) using expression in RASTER CALCULATOR tool; use FOCAL STATISTICS tool to calculate mean of MGE raster within circular sampling unit	Equations in Table 4
	% MGE	Extract DDE pixels ≥2.40 (marginal or better) using expression in RASTER CALCULATOR tool, then use RASTER CALCULATOR to calculate percent area of MGE within circular sampling unit	Equations in Table 4
Human disturbance	Distance to nearest road open to motorized use by public	Select all roads open to public with the SELECT tool; use EUCLIDEAN DISTANCE tool to calculate distance from center pixel of circular sampling unit to nearest pixel from roads raster grid	Various; primary base layer was Ground Transportation (GTRN) roads database from Bureau of Land Management; updated based on local knowledge about road conditions
Vegetation	Distance to cover-forage edge	Create cover-forage patches (see text); create line feature representing edge between patches; use EUCLIDEAN DISTANCE tool to calculate	GNN: CANCOV, STNDHGT

Model set	Covariate name ^b	Derivation	Data source
Physical	% slope	distance to nearest edge from center pixel of circular sampling unit (distance-to-edge grid) Convert DEM raster to percent slope using SLOPE (Spatial Analyst) tool; use FOCAL STATISTICS tool to calculate mean percent slope of raster within circular sampling unit	DEM (http://ned.usgs.gov/)
	Density of open roads	Select all roads open to public with the SELECT tool; use LINE DENSITY tool to calculate road density	Various; primary base layer was Ground Transportation (GTRN) roads database obtained from Bureau of Land Management; updated based on local knowledge about road condition (i.e., open to public, closed because of mudslides)

^a ArcGIS Desktop version 9.3 and 10.0 with Spatial Analyst extension (Environmental Systems Research Institute, Inc.).

^b Abbreviations: CANCOV, canopy cover of live trees; DDE, dietary digestible energy (kcal/g); DEM, digital elevation model; GNN, gradient nearest neighbor, model region 200; MGE, marginal, good, or excellent DDE (see Cook et al. 2004); IMAP_LAYER, number of tree canopy layers present; PNV, potential natural vegetation; QMDA_DOM, quadratic mean diameter of all dominant and co-dominant trees; STNDHGT, stand height, calculated as average height of all dominant and co-dominant trees; TPH_GE_3, density of live trees (stems/ha) ≥ 2.5 cm dbh; TPHH_GE_3, density of hardwoods (stems/ha) ≥ 2.5 cm dbh.

^c 350 m-radius circular sampling unit used for model development areas and for calculation of mean values for moving window analyses in validation modeling areas.

^d We calculated proportion of total trees that are hardwoods, a variable used in the biomass equations, by dividing hardwood tree density (TPHH_GE_3) by total tree density (TPH_GE_3).

Table B3. Existing vegetation types considered non-habitat and masked from analysis in elk nutrition and habitat-use models developed for western Oregon and Washington, USA.

Ecological system ^a	Area (ha)	% Area
Barren land (rock/sand/clay)	517	<0.01
Developed, high intensity	53,467	0.46
Developed, low intensity	353,216	3.01
Developed, medium intensity	53,303	0.45
Developed, open space	189,763	1.62
North American alpine ice field	27,489	0.23
North Pacific alpine and subalpine bedrock and scree	20,585	0.18
North Pacific coastal cliff and bluff	247	<0.01
North Pacific maritime eelgrass bed	428	<0.01
North Pacific montane massive bedrock, cliff and talus	41,612	0.35
North Pacific volcanic rock and cinder land	14,837	0.13
Open water	111,876	0.95
Perennial ice/snow	1,519	0.01
Rocky Mountain alpine bedrock and scree	89	<0.01
Rocky Mountain cliff, canyon and massive bedrock	2,816	0.02
Temperate Pacific intertidal mudflat	2,340	0.02
Unconsolidated shore	12,748	0.11
Total	886,853	7.56

^a Ecological system code for existing vegetation type (from LEMMA project: <http://www.fsl.orst.edu/lemma/main.php?project=nwfp&id=studyAreas>).

Table B4. Values of covariates (mean and range) used to create Westside elk habitat-use and nutrition models for 5 modeling data sets from western Oregon and Washington, USA.

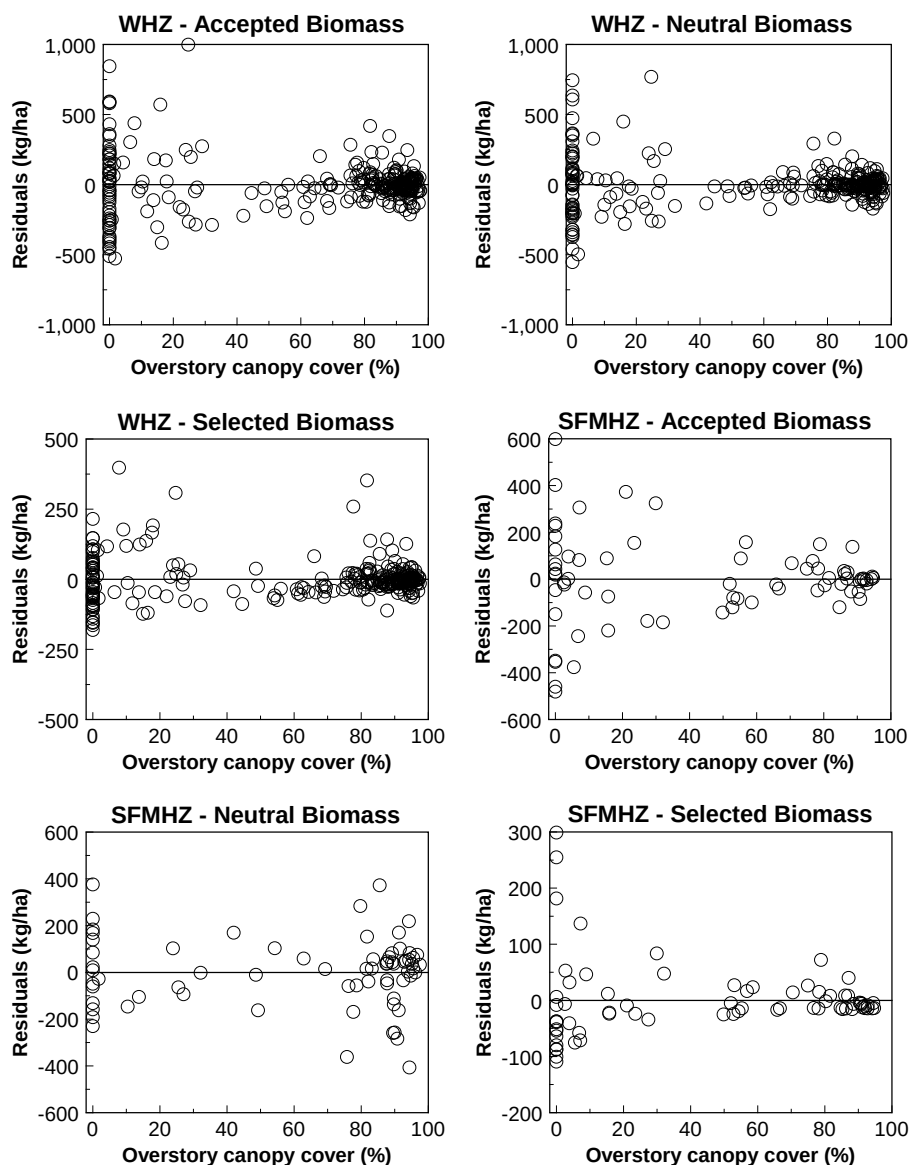
Covariate (unit)	Green-Cedar 2008	Pysht 2009	White River 2004	White River 2005	White River 2007
Accepted biomass (kg/ha)	174 (0–707)	352 (46–707)	138 (3–683)	178 (5–640)	181 (5–683)
DDE ^a (kcal/g)	2.53 (2.40–2.93)	2.48 (2.31–2.65)	2.56 (2.41–2.93)	2.58 (2.41–2.92)	2.58 (2.41–2.93)
MGE ^b (kcal/g)	2.53 (2.40–2.93)	2.59 (2.42–2.66)	2.57 (2.42–2.93)	2.58 (2.42–2.92)	2.59 (2.42–2.93)
% MGE	97.35 (41.38–100)	54.83 (4.62–100)	96.24 (27.85–100)	95.30 (17.77–100)	95.06 (17.77–100)
Distance to open road (m)	4,769 (0–12,431)	1,574 (0–5,357)	2,115 (0–9,347)	1,819 (0–5,414)	2,049 (0–7,241)
Distance to cover-forage edge (m)	506 (0–2,460)	121 (0–1,300)	376 (0–2,074)	288 (0–1,842)	263 (0–1,745)
% slope	28.92 (0–76.87)	16.00 (1.39–65.53)	41.39 (1.24–100)	34.73 (1.23–87.69)	39.40 (1.23–100)

^a Dietary digestible energy (kcal/g).

^b Marginal, good, or excellent categories of DDE; values ≥ 2.4 .

APPENDIX C. PLOTS OF RESIDUALS FROM PREDICTION EQUATIONS FOR FORAGE BIOMASS

Residuals from prediction equations (Table 6) for accepted, neutral, and selected biomass were plotted with overstory canopy cover to identify heteroscedasticity and to evaluate our success in accounting for non-linearity. Data were collected in the western hemlock zone (WHZ) and the Pacific silver fir and mountain hemlock zones (SFMHZ) in western Oregon and Washington, 2000–2002.



APPENDIX D. REGRESSION MODELS TO EVALUATE PROBABILITY OF ELK USE

All logistic regression models, organized by model set, used to evaluate probability of use by elk during summer for 5 model development data sets in western Oregon and Washington, USA. We evaluated models with Akaike's Information Criterion (AIC) and Akaike weights (w_i). Data set name includes the study area (PY = Pysht; WR = White River; GC = Green-Cedar) and the last 2 digits of the year.

Model set	Data set	Model number	Model	AIC	w_i	K^a
Nutrition	GC08	1	DDE ^b	5,132.175	0.456	3
		2	AB ^c	5,132.951	0.309	3
		3	MGE, ^d %MGE, MGE $\times$ %MGE	5,133.496	0.235	5
	PY09	1	DDE	1,081.136	0.372	3
		2	AB	1,081.381	0.329	3
		3	MGE, %MGE, MGE $\times$ %MGE	1,081.580	0.298	5
	WR04	3	MGE, %MGE, MGE $\times$ %MGE	5,143.024	0.995	5
		1	DDE	5,153.818	0.005	3
		2	AB	5,182.784	<0.001	3
	WR05	1	DDE	2,207.810	0.534	3
		2	AB	2,208.638	0.353	3
		3	MGE, %MGE, MGE $\times$ %MGE	2,210.928	0.112	5
	WR07	2	AB	5,474.779	0.511	3
		3	MGE, %MGE, MGE $\times$ %MGE	5,474.892	0.483	5
		1	DDE	5,483.633	0.006	3
Human disturbance	GC08	1	Distance to open road ^e	5,139.023	0.720	3
		2	(Distance to open road) ²	5,140.910	0.280	4
	PY09	1	Distance to open road	1,106.362	0.638	3
		2	(Distance to open road) ²	1,107.497	0.362	4
	WR04	2	(Distance to open road) ²	5,199.115	0.994	4
		1	Distance to open road	5,209.218	0.006	3
	WR05	2	(Distance to open road) ²	2,224.345	0.551	4
		1	Distance to open road	2,224.757	0.449	3
	WR07	1	Distance to open road	5,492.623	0.730	3

Nutrition + (vegetation and/or physical)	GC08	2	(Distance to open road) ²	5,494.610	0.270	4
		2	DDE, distance to cover-forage edge, slope	5,111.601	0.873	5
		1	DDE, slope	5,115.462	0.127	4
	PY09	3	DDE, distance to cover-forage edge	5,126.100	0.001	4
		1	DDE, slope	1,066.048	0.579	4
		2	DDE, distance to cover-forage edge, slope	1,066.687	0.421	5
	WR04	3	DDE, distance to cover-forage edge	1,082.074	<0.001	4
		2	DDE, distance to cover-forage edge, slope	5,106.355	0.972	5
		1	DDE, slope	5,113.444	0.028	4
	WR05	3	DDE, distance to cover-forage edge	5,145.650	<0.001	4
		1	DDE, slope	2,180.626	0.729	4
		2	DDE, distance to cover-forage edge, slope	2,182.604	0.271	5
	WR07	3	DDE, distance to cover-forage edge	2,206.834	<0.001	4
		2	DDE, distance to cover-forage edge, slope	5,386.633	0.667	5
		1	DDE, slope	5,388.025	0.333	4
Human disturbance + (vegetation and/or physical)	GC08	3	DDE, distance to cover-forage edge	5,467.943	<0.001	4
		3	Distance to open road, distance to cover-forage edge, slope	5,104.795	>0.999	5
		1	Distance to open road, slope	5,126.607	<0.001	4
	PY09	2	Distance to open road, distance to cover-forage edge	5,127.149	<0.001	4
		1	Distance to open road, slope	1,102.463	0.543	4
		3	Distance to open road, distance to cover-forage edge, slope	1,103.102	0.395	5
	WR04	2	Distance to open road, distance to cover-forage edge	1,106.788	0.062	4
		3	Distance to open road, distance to cover-forage edge, slope	5,132.589	>0.999	5
		2	Distance to open road, distance to cover-forage edge	5,169.631	<0.001	4
	WR05	1	Distance to open road, slope	5,178.014	<0.001	4
		3	Distance to open road, distance to cover-forage edge, slope	2,199.049	0.945	5
		1	Distance to open road, slope	2,204.730	0.055	4
		2	Distance to open road, distance to cover-forage edge	2,215.938	<0.001	4

Nutrition + human disturbance + (vegetation and/or physical)	WR07	3	Distance to open road, distance to cover-forage edge, slope	5,371.231	>0.999	5
		1	Distance to open road, slope	5,409.320	<0.001	4
		2	Distance to open road, distance to cover-forage edge	5,466.124	<0.001	4
	GC08	3	DDE, distance to open road, distance to cover-forage edge, slope	5,102.532	0.990	6
		2	DDE, distance to open road, slope	5,111.663	0.010	5
		1	DDE, distance to open road, distance to cover-forage edge	5,128.094	<0.001	5
	PY09	2	DDE, distance to open road, slope	1,065.397	0.603	5
		3	DDE, distance to open road, distance to cover-forage edge, slope	1,066.239	0.396	6
		1	DDE, distance to open road, distance to cover-forage edge	1,077.767	0.001	5
	WR04	3	DDE, distance to open road, distance to cover-forage edge, slope	5,087.763	0.894	6
		2	DDE, distance to open road, slope	5,092.033	0.106	5
		1	DDE, distance to open road, distance to cover-forage edge	5,140.555	<0.001	5
	WR05	2	DDE, distance to open road, slope	2,176.349	0.723	5
		3	DDE, distance to open road, distance to cover-forage edge, slope	2,178.270	0.277	6
		1	DDE, distance to open road, distance to cover-forage edge	2,207.858	<0.001	5
Final set of candidate models	WR07	3	DDE, distance to open road, distance to cover-forage edge, slope	5,361.212	0.985	6
		2	DDE, distance to open road, slope	5,369.609	0.015	5
		1	DDE, distance to open road, distance to cover-forage edge	5,467.984	<0.001	5
	GC08	6	DDE, distance to open road, distance to cover-forage edge, slope	5,102.532	0.750	6
		5	Distance to open road, distance to cover-forage edge, slope	5,104.795	0.242	5

PY09	4	DDE, distance to cover-forage edge, slope	5,111.601	0.008	5
	1	DDE	5,132.175	<0.001	3
	3	DDE, distance to open road	5,133.410	<0.001	4
	2	Distance to open road	5,139.023	<0.001	3
	6	DDE, distance to open road, distance to cover-forage edge, slope	1,066.239	0.553	6
	4	DDE, distance to cover-forage edge, slope	1,066.687	0.442	5
WR04	3	DDE, distance to open road	1,076.302	0.004	4
	1	DDE	1,081.136	<0.001	3
	5	Distance to open road, distance to cover-forage edge, slope	1,103.102	<0.001	5
	2	Distance to open road	1,106.362	<0.001	3
	6	DDE, distance to open road, distance to cover-forage edge, slope	5,087.763	>0.999	6
	4	DDE, distance to cover-forage edge, slope	5,106.355	<0.001	5
WR05	5	Distance to open road, distance to cover-forage edge, slope	5,132.589	<0.001	5
	3	DDE, distance to open road	5,148.597	<0.001	4
	1	DDE	5,153.818	<0.001	3
	2	Distance to open road	5,209.218	<0.001	3
	6	DDE, distance to open road, distance to cover-forage edge, slope	2,178.270	0.897	6
	4	DDE, distance to cover-forage edge, slope	2,182.604	0.103	5
WR07	5	Distance to open road, distance to cover-forage edge, slope	2,199.049	<0.001	5
	1	DDE	2,207.810	<0.001	3
	3	DDE, distance to open road	2,208.344	<0.001	4
	2	Distance to open road	2,224.757	<0.001	3
	6	DDE, distance to open road, distance to cover-forage edge, slope	5,361.212	0.993	6
	5	Distance to open road, distance to cover-forage edge, slope	5,371.231	0.007	5
	4	DDE, distance to cover-forage edge, slope	5,386.633	<0.001	5

1	DDE	5,483.633	<0.001	3
3	DDE, distance to open road	5,485.131	<0.001	4
2	Distance to open road	5,492.623	<0.001	3

^a Number of parameters in model.

^b Mean dietary digestible energy (kcal/g) within circular sampling unit.

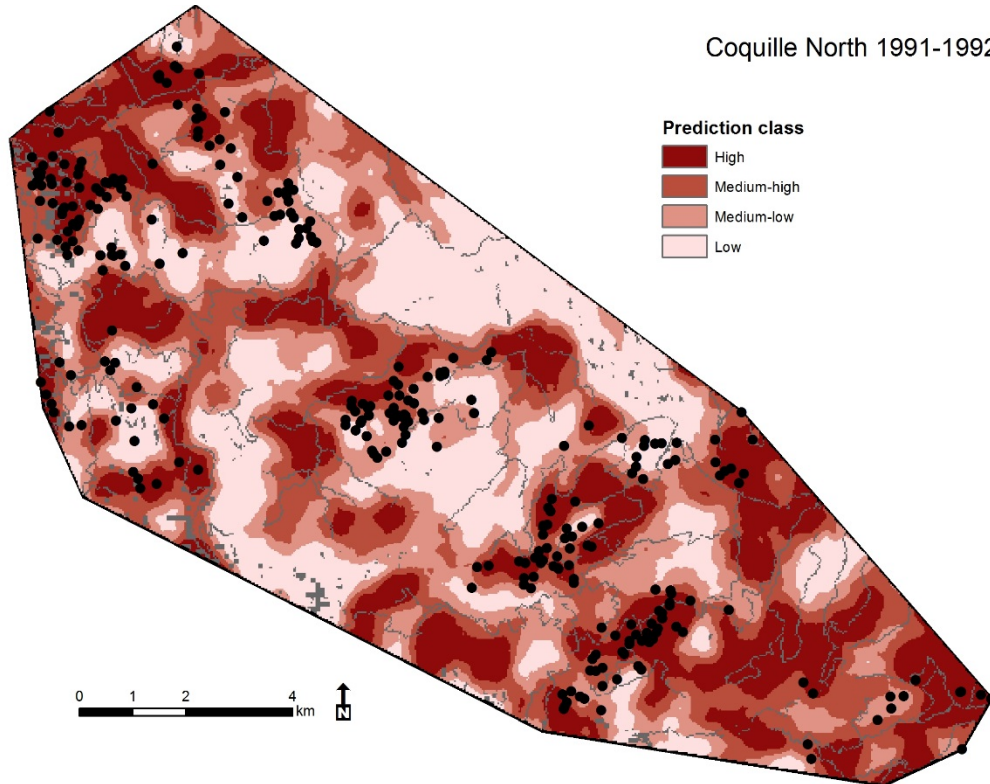
^c Mean accepted biomass of elk forage species (kg/ha) within circular sampling unit.

^d Mean of marginal, good, or excellent categories of DDE (i.e., values ≥ 2.4) within a circular sampling unit and percentage of sampling unit in MGE.

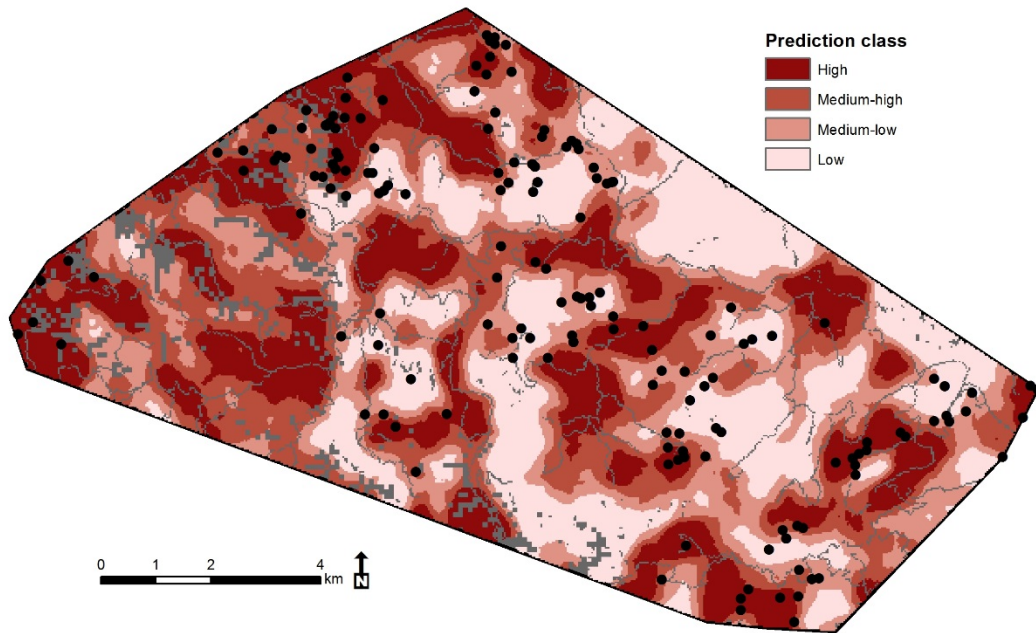
^e Distance to nearest road open to motorized use by public.

APPENDIX E. PREDICTIVE MAPS OF RELATIVE PROBABILITY OF USE BY ELK

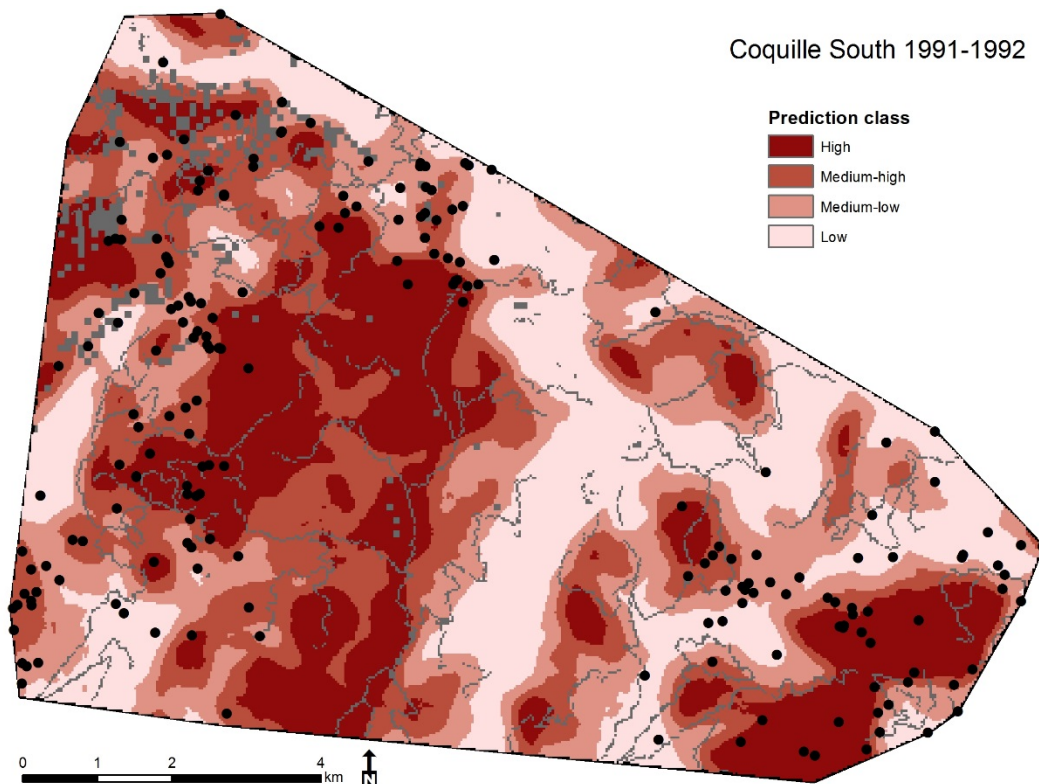
We developed maps that display relative probability of elk use for 8 model validation data sets in western Oregon and Washington, USA, classified into 4 equal-area prediction bins for display: low, medium-low, medium-high, and high. Dots represent observed locations of elk used to validate the habitat-use model. Masked areas represent non-habitat, such as rock or water, and are displayed as gray in the maps.

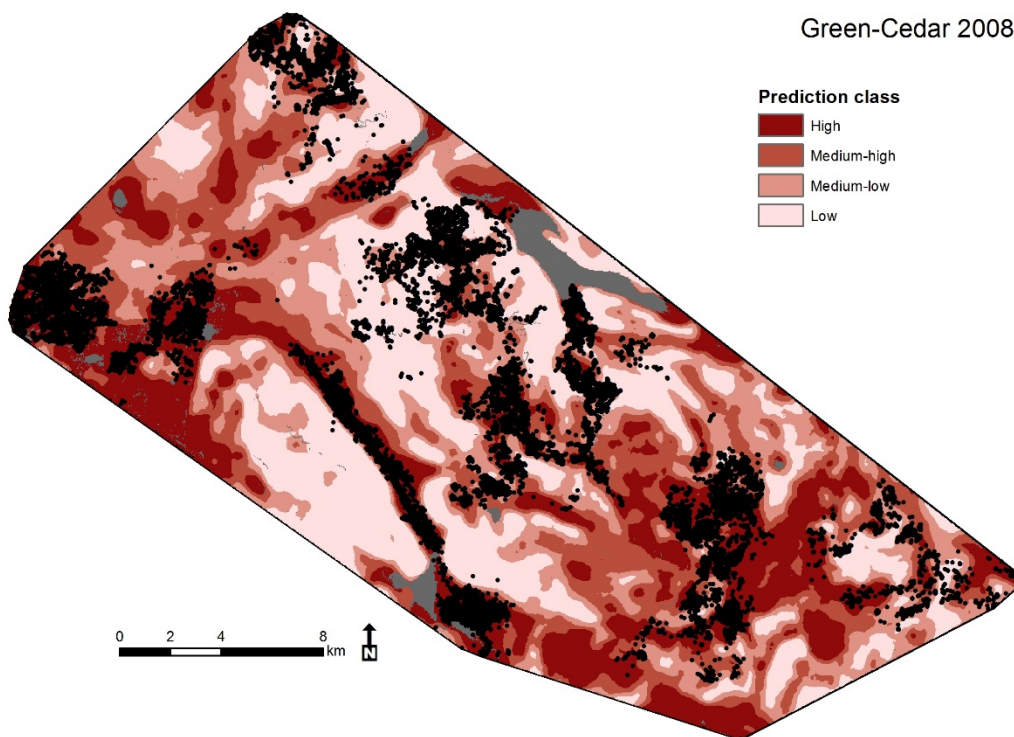
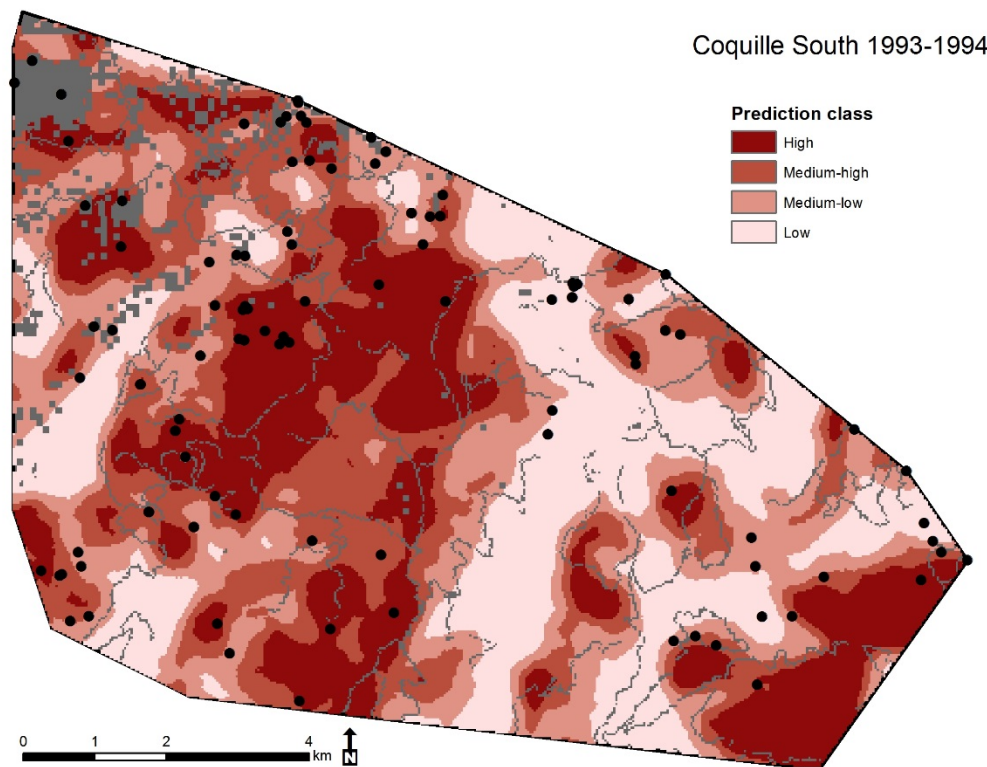


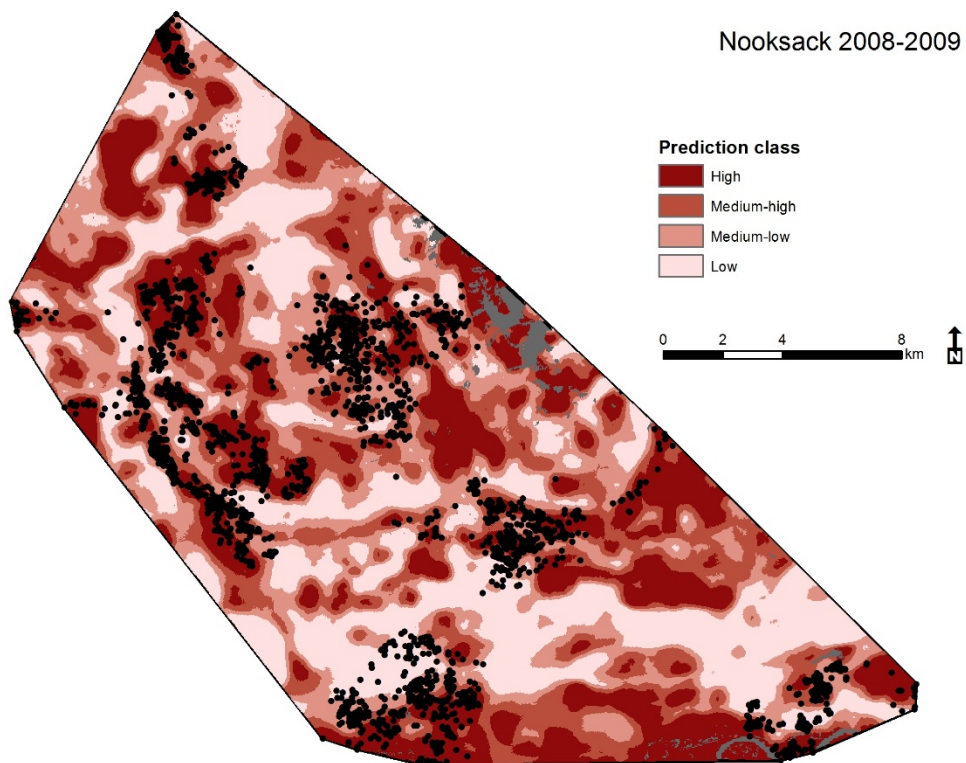
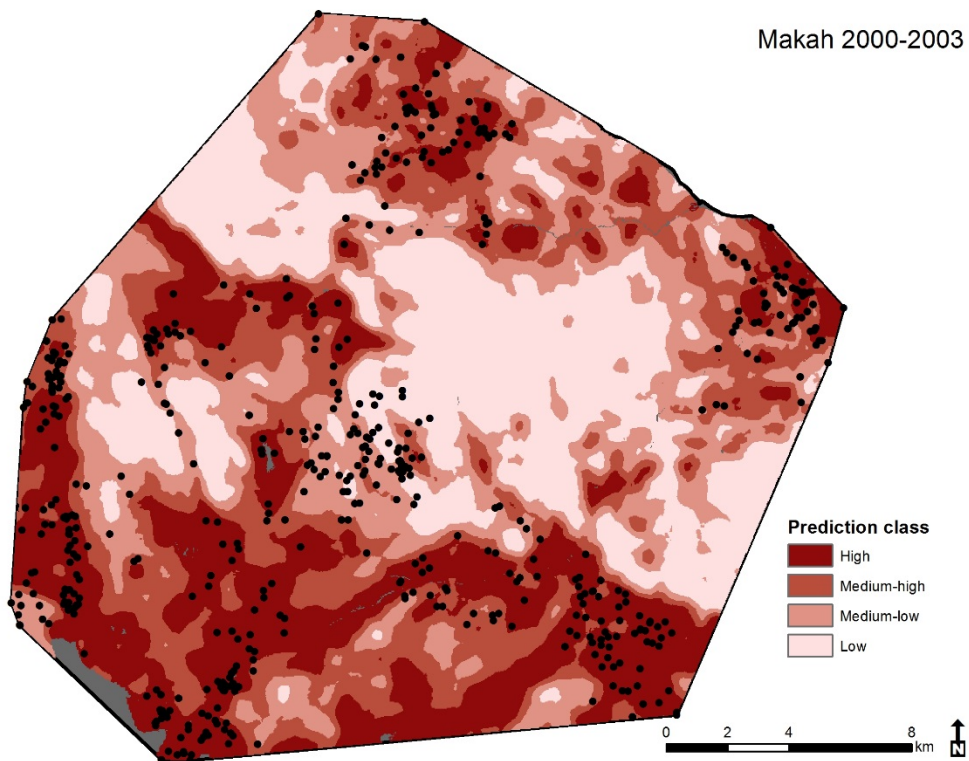
Coquille North 1993-1994

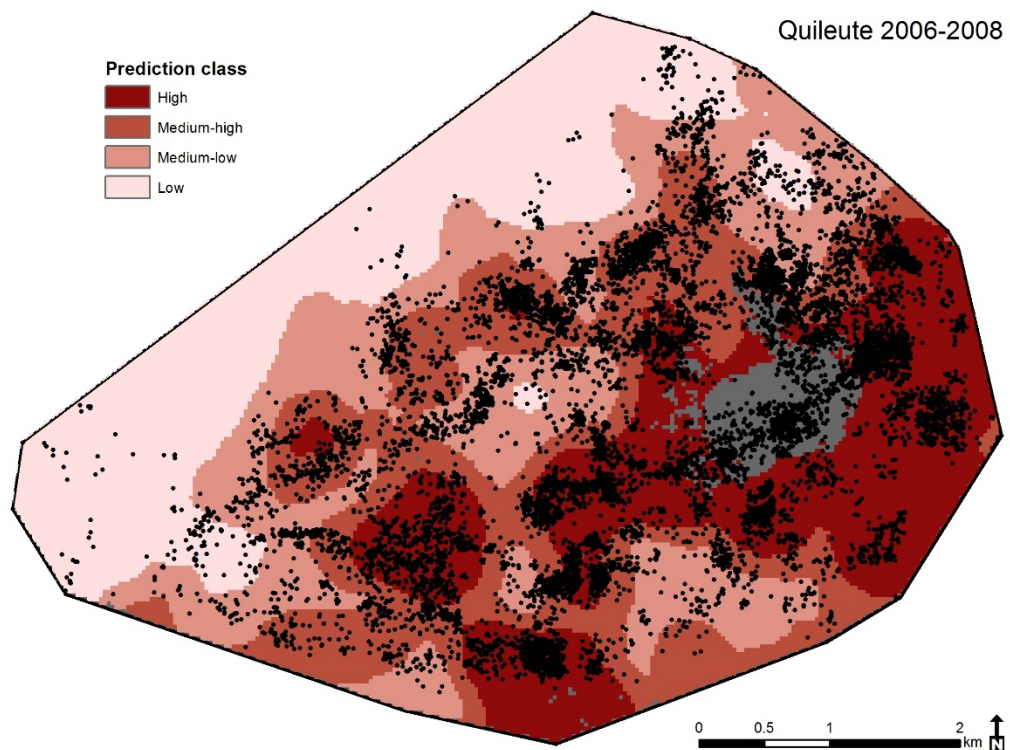


Coquille South 1991-1992









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