THE CONDOR
Ornithological Applications
AmericanOrnithology.org

Volume 118, 2016, pp. 766–790
DOI: 10.1650/CONDOR-16-86.1

RESEARCH ARTICLE

Transferability of habitat suitability models for nesting woodpeckers associated with wildfire

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Submitted May 13, 2016; Accepted August 10, 2016; Published October 19, 2016

ABSTRACT

Following wildfire, forest managers are challenged with meeting both socioeconomic demands (e.g., salvage logging) and mandates requiring habitat conservation for disturbance-associated wildlife (e.g., woodpeckers). Habitat suitability models for nesting woodpeckers can be informative, but tests of model transferability are needed to understand how broadly models developed at one location can be applied to inform post-fire forest management at other locations. We developed habitat suitability models and tested their transferability for 2 disturbance-associated woodpecker species, Black-backed (*Picoides arcticus*) and Lewis's (*Melanerpes lewis*) woodpecker. Habitat suitability models consisted of weighted logistic regression models comparing environmental conditions at nest versus non-nest sites. We developed models at each of 3 wildfire locations in Washington, Oregon, and Idaho, and then examined predictive performance for each model at alternate ("application") locations. Models generally discriminated nest from non-nest sites well at locations where they were developed but performance was variable at application locations, indicating limited transferability. Models for Black-backed Woodpecker and those that included field-collected environmental covariates exhibited greater transferability than models for Lewis's Woodpecker and those that only included remotely sensed covariates. Transferability was also generally poor between Oregon and the other 2 locations. Limitations to model transferability observed in this study suggest models developed at any one wildfire location are unlikely to be generally applicable across the entire range of Black-backed and Lewis's woodpeckers. Generally applicable models to inform post-fire forest management will therefore likely require integration of data from multiple wildfire locations.

Keywords: disturbance-associated woodpeckers, Black-backed Woodpecker, habitat suitability model, Lewis's Woodpecker, *Picoides arcticus*, *Melanerpes lewis*, breeding habitat, model transferability, predictive performance, wildfire, forest management, salvage logging

Habilidad de transferencia de los modelos de idoneidad de hábitat de pájaros carpinteros anidantes asociados con fuegos naturales

RESUMEN

Después de los incendios forestales, los administradores ambientales tienen el desafío de atender las demandas socioeconómicas (e.g. tala de salvamento) y los mandatos que requieren la conservación del hábitat para animales silvestres asociados con el disturbio (e.g. pájaros carpinteros). Los modelos de idoneidad de hábitat de pájaros carpinteros anidantes pueden ser informativos, pero se necesitan pruebas sobre la habilidad de transferencia de dichos modelos para entender cómo modelos desarrollados para una localidad pueden ser aplicados para informar decisiones de manejo luego de incendios en otras localidades. Desarrollamos modelos de idoneidad de hábitat y probamos su habilidad de transferencia para dos especies de carpinteros asociados con disturbios, *Picoides arcticus* y *Melanerpes lewis*. Los modelos de idoneidad de hábitat consistieron de modelos ponderados de regresión logística que comparan las condiciones ambientales de los sitios de anidación con las de sitios de no anidación. Desarrollamos modelos en cada una de tres localidades con incendios naturales en Washington, Oregon y Idaho, y luego examinamos la habilidad predictiva de cada modelo en localidades alternas ("aplicación"). Los modelos generalmente discriminaron bien los sitios con y sin nidos en las localidades donde fueron desarrollados pero su desempeño fue variable en las localidades de aplicación, lo que indica una habilidad de transferencia limitada. Los modelos para *P. arcticus* y los que incluyeron covariables ambientales medidas en campo tuvieron mayor habilidad de transferencia que los modelos para *M. lewis* y aquellos que solo incluyeron covariables medidas por sensores remotos. Sin embargo, la habilidad de transferencia generalmente fue pobre entre Oregon y las otras dos localidades. Las limitaciones en la habilidad de transferencia de los modelos observadas en este estudio sugieren que no es probable que los modelos desarrollados en una localidad con incendios naturales sean aplicables en general a través de la distribución geográfica de *P. arcticus* y *M. lewis*. El desarrollo de modelos que puedan ser aplicados generalmente para informar decisiones de manejo posteriores a incendios probablemente requerirá la integración de datos de múltiples localidades donde hayan sucedido incendios.

Palabras clave: desempeño predictivo, habilidad de transferencia de modelos, hábitat reproductivo, incendios naturales, manejo de bosques, *Melanerpes lewis*, modelos de idoneidad de hábitat, pájaros carpinteros asociados a hábitats con disturbio, *Picoides arcticus*, tala de salvamento

INTRODUCTION

In lower elevation, dry conifer forests of western North America, wildfire strongly shapes vegetation structure and composition along with associated biological communities. Salvage logging in burned forests provides economic activity for local communities, but can degrade habitat quality for disturbance-associated wildlife (Saab et al. 2005, Lindenmayer and Noss 2006, Lindenmayer et al. 2008). In particular, woodpeckers and other cavity-nesting species benefit from trees that are killed, damaged, or weakened by fire for nesting and foraging (Russell et al. 2007, Saab et al. 2007). Anthropogenic land use and human-induced climate change have altered and continue to reshape natural fire regimes (Schoennagel et al. 2004, Fulé et al. 2012, Hessburg et al. 2015), so federal and state agencies are concerned with conservation of woodpeckers associated with recently disturbed forests. Salvage logging can negatively impact woodpeckers by removing trees killed by fire (Hutto and Gallo 2006, Saab et al. 2007), so forest managers must consider socioeconomic demands with mandates requiring maintenance of post-fire habitat for woodpeckers. To meet these needs, managers must identify suitable habitat for fire-associated woodpecker species.

In the western United States, a number of fire-associated woodpecker species use a range of habitats within burned forests. Black-backed Woodpeckers (*Picoides arcticus*) nest primarily in burned forests (Dixon and Saab 2000, Hutto 2008; but see Bonnot et al. 2009 and Fogg et al. 2014). Lewis's (*Melanerpes lewis*) and White-headed woodpeckers (*P. albolvartus*) are less specialized but some evidence suggests burned forests may represent important source habitat for maintaining population persistence (Saab and Vierling 2001, Wightman et al. 2010, Hollenbeck et al. 2011). Different species favor different environmental conditions within burned forests, so conserving habitat representing various conditions could benefit multiple woodpecker species along with a range of other species (Saab et al. 2009). Such efforts would require species-specific information capable of informing post-fire forest management planning. For example, Black-backed and Lewis's woodpeckers are found nesting in moderate- to high-severity burned forests (Russell et al. 2007, Latif et al. 2013), while White-headed Woodpeckers use low- to moderate-severity burns adjacent to unburned forests (Wightman et al. 2010). Additionally, Black-backed Woodpeckers were reported to nest in areas with relatively high snag densities of smaller diameters, and with moderately high pre-fire canopy cover (> 40–70%; Saab et al. 2009). In contrast, Lewis's Woodpeckers select more open post-fire forests with moderate snag densities of larger diameters (Saab et al. 2009, Vierling et al. 2013).

Researchers use habitat suitability models (sometimes known as species distribution models) to quantify habitat and predict species distributions to guide land management decisions aimed at species conservation (Guisan et al. 2013). Models quantify environmental relationships with known species occurrences, and translate these relationships into predictions of species distributions. Models may also provide habitat suitability indices (HSIs; 0–1 range) that at minimum indicate relative likelihood of species occurrence (0 = least likely, 1 = most likely). Interpretation of HSIs and their value for ecological inference is the subject of ongoing debate and depends at least in part on modeling technique and data used for model development (Royle et al. 2012, Lele et al. 2013, McDonald 2013, Merow and Silander 2014, Guillera-Arroita et al. 2015). Nevertheless, to inform habitat conservation, models are ultimately expected to discriminate where species are most, versus least, likely to occur within relevant project areas.

How we develop and evaluate habitat models must reflect the intended application. We can use models to identify areas with suitable habitat where managers could restrict logging to conserve habitat (i.e. to identify habitat reserves). Predictive habitat maps that provide continuous coverage of burned areas and severity would be most desirable for this application. Such maps typically require remotely sensed environmental data (e.g., Franklin 2009, Elith et al. 2010) that are typically limited to coarse resolution and information content (Kerr and Ostrovsky 2003). Thus, restricting models to remotely sensed data can limit performance by limiting their ability to quantify key relationships governing species distributions at finer resolutions (Russell et al. 2007). Conversely, including field-measured data can improve performance (Russell et al. 2007). Doing so may preclude habitat mapping over broad spatial extents, but field-collected data may provide finer-resolution information useful for logging prescriptions to maintain or improve habitat suitability.

Regardless of the particular application, models must continually be applied to new locations as new wildfires occur to inform post-fire habitat management (Latif et al. 2013). Biotic interactions, local adaptation, and behavioral rules governing habitat selection, however, can give rise to spatial variability in environmental relationships, which can limit how broadly models can be applied (Araújo and Luoto 2007, Morrison 2012, Aarts et al. 2013). Several habitat suitability models for wildfire-associated woodpeckers have been developed (Russell et al. 2007, Saab et al. 2009, Wightman et al. 2010, Tingley et al. 2016). Due to funding limitations and the unpredictability of wildfire, these models typically represent habitat relationships measured at individual locations (except see Tingley et al. 2016), potentially limiting model applicability. Such concerns are common for predictive habitat models (Morrison 2012, Aarts et al. 2013), raising the need to evaluate applicability, specifically by testing spatial transferability (i.e. how well predictions can be transferred to new locations; Randin et al. 2006, Wenger and Olden 2012) before applying them to inform management. Analysts routinely test predictive performance using randomly selected data subsets withheld during model development (Guisan and Zimmermann 2000). To fully evaluate predictive performance, however, test data are best collected beyond the spatial extent of model development, which allows evaluation of model transferability across locations (Heikkinen et al. 2012, Wenger and Olden 2012, Bahn and McGill 2013).

We developed habitat suitability models and evaluated transferability for 2 wildfire-associated woodpecker species, Black-backed Woodpecker and Lewis's Woodpecker, using nest site data from 3 wildfire locations in Washington, Oregon, and Idaho. These 2 species were selected because they strongly favor post-fire forests for nesting and they represent a range of snag densities and diameters, from high snag densities of smaller diameters to moderate snag densities of larger diameters (e.g., Saab et al. 2009). Conservation efforts that target both species will incorporate diverse habitat conditions generated by wildfire that will likely provide habitat for other cavity-dwelling vertebrate species (Saab et al. 2007, 2009). For each species, we developed a model using data from each location where the species occurred and then measured predictive performance at alternate locations. We developed models using exclusively remotely sensed covariates to support predictive habitat mapping, and combinations of remotely sensed and field-collected covariates to better inform management prescriptions. We considered whether models developed at one location could accurately quantify habitat to generally inform post-fire habitat management.

METHODS

Study Locations

We developed and evaluated habitat suitability models at 3 locations in the northwestern United States. Locations are

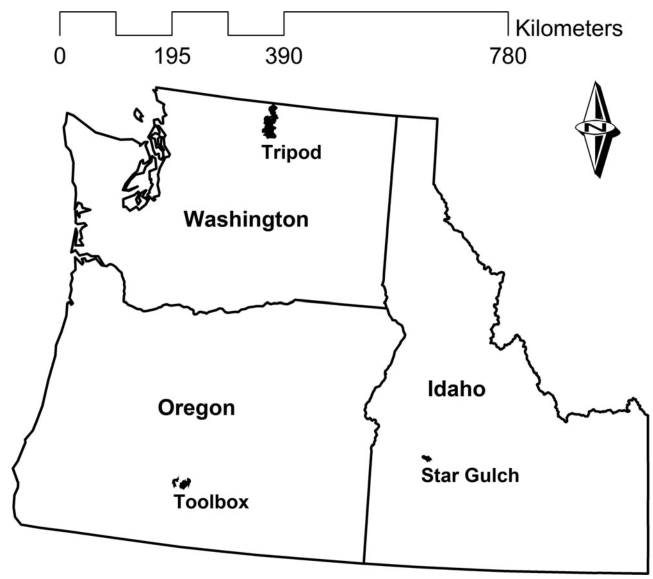

FIGURE 1. Wildfire study locations. Maps shows the 3 study locations where habitat suitability models were developed and evaluated for wildfire-associated woodpeckers (USA). The Tripod Fire occurred in Washington (WA), the Toolbox Fires (Toolbox and Silver Fires) occurred in Oregon (OR), and the Star Gulch Fire occurred in Idaho (ID).

dry mixed-conifer forest dominated by ponderosa pine strongly influenced by historically recurring wildfire (Agee 1993, Hessburg et al. 2005, Saab et al. 2005). Our 3 study locations experienced wildfires ranging from ~12,000 to 99,000 ha between the years 1994 and 2006.

Tripod Fire. The Tripod wildfire (2006) burned 99,349 ha in north-central Washington, USA (48°40′N, 120°0′W; Figure 1). Elevation ranged from 679 m to 2,536 m. This fire burned in the Okanogan-Wenatchee National Forest, which is dominated by ponderosa pine (*Pinus ponderosa*; Hollenbeck et al. 2013), although the most common snag species observed at sites measured here were Douglas fir (*Pseudotsuga menziesii*) and lodgepole pine (*Pinus contorta*), followed by ponderosa pine. Common understory species characterizing forests of this region include snowberry (*Symphoricarpos albus*), spirea (*Spiraea betulifolia*), serviceberry (*Amelanchier alnifolia*), chokecherry (*Prunus virginiana*), bluebunch wheatgrass (*Pseudoroegneria spicata*), and Idaho fescue (*Festuca idahoensis*). Salvage logging occurred in 2–3% of the sampled landscape (Appendix A).

Star Gulch Fire. The Star Gulch wildfire (1994) burned 12,358 ha in southwestern Idaho, USA (43°35′N, 115°42′W; Figure 1). Elevation ranged from 1,130 m to 2,300 m. Ponderosa pine and Douglas fir were the most common snag species in the burned area. Shrubs common in the understory and in forest openings included sagebrush (*Artemisia tridentata*), ninebark (*Physocarpus malvaceus*), and ceanothus (*Ceanothus velutinus*) (John-

TABLE 1. Sample sizes and extent at 3 wildfire locations where habitat suitability models were developed and evaluated. Models were developed for nesting Black-backed Woodpeckers (BBWO) and Lewis's Woodpeckers (LEWO). Wildfire locations were in the states of Washington (WA), Oregon (OR), and Idaho (ID) in the USA.

					n		
Wildfire location	Ignition year	Years surveyed	Wildfire extent (ha)	Sampling extent (ha)	BBWO nests	LEWO nests	non-nest
Tripod, WA	2006	2008–2009	99,349	748 & 956[a]	26	0	68
Toolbox, OR	2002	2003–2007	33,427	857[b]	249	47	484, 499[c]
Star Gulch, ID	1994	1995–1998	12,358	942	36	50	47

[a] Unit boundaries were adjusted between years at Tripod. Sampled area was 748 and 956 ha in 2008 and 2009, respectively.
[b] Some units were added in later years at Toolbox. Reported value reflects the maximum sampled area in any one year.
[c] We retained 484 and 499 non-nest sites for Black-backed and Lewis's woodpeckers, respectively, after excluding non-nest sites ≤ 30 m from nearest nests.

son et al. 2000, Saab et al. 2004). Our study units within this location were unlogged, but salvage logging occurred in surrounding areas.

Toolbox Fire. The Toolbox and Silver wildfires (2002; hereafter Toolbox Fire) burned 23,482 ha and 9,945 ha, respectively, in south-central Oregon, USA (Figure 1). Elevation ranged from 1,312 m to 2,172 m. This fire burned in the Fremont-Winema National Forest, which is dominated by ponderosa pine (Hollenbeck et al. 2013). Dominant tree species in the burned area consisted of pine (*P. ponderosa, P. contorta*) and white fir (*Abies concolor*). Common understory species characterizing forests of this region are similar to the Tripod location. Salvage logging occurred in 20–26% of the sampled landscape (Appendix Table 8).

Nest and Non-Nest Sites

We surveyed for occupied Black-backed and Lewis's woodpecker nest cavities within the Star Gulch, Tripod, and Toolbox wildfires during years 1–5 post-fire. We systematically searched for nest cavities during spring nesting seasons along belt transects (averaged 0.2 × 1 km; Dudley and Saab 2003). Belt transects were arranged to provide complete coverage of all areas within study unit boundaries. Although we mainly searched within study unit boundaries, we occasionally found nests up to 250 m outside unit boundaries when following individual birds, and these were included in our analysis. The area sampled covered approximately 800–1,000 ha at each location (Table 1).

We quantified nest site selection by measuring and comparing environmental data at nest and non-nest sites. Non-nest sites were randomly located within study unit boundaries and excluded sites within 30 m of any nest site. Thus, non-nest sites represented available habitat that was not used for nesting. At Tripod and Star Gulch locations, we collected environmental data at nest and non-nest sites using field and remotely sensed measurements. At these locations, we measured as many non-nest sites as possible given available funding and personnel (Table 1), and non-nest coordinates were generated using a random point generator in ArcGIS (ESRI 2011). At Toolbox, non-nest field measurements were not recorded in all study units and were therefore insufficient to characterize habitat availability. Consequently, we developed Toolbox models using only remotely sensed data, which we compiled for an arbitrarily large sample of non-nest sites (Table 1) selected randomly from a 30-m point grid that spanned study units.

Environmental Data

Remotely sensed environmental data described topography, burn severity, and pre-fire canopy cover (Table 2). The relevance of these features was described previously (Raphael and White 1984, Li and Martin 1991, Russell et al. 2007, Saab et al. 2009, Saracco et al. 2011). All remotely sensed environmental data were 30 m × 30 m resolution (pixel size). Topographic variables represented attributes of pixels containing nest or non-nest sites. All other variables represented either local-scale (3 × 3 cells; 0.8 ha) or landscape-scale (1-km–radius circle; 314 ha) neighborhoods centered on the nest or non-nest sites. Landscape-scale neighborhoods approximated home-range sizes of many woodpecker species that depend on snags for nesting and foraging during the nesting season (Saab et al. 2004). Data sources were USGS National Elevation Dataset for topography (1 arc-second; available at http://viewer.nationalmap.gov/viewer/) and Monitoring Trends in Burn Severity for burn severity (ΔNBR; available at http://mtbs.gov). Pre-fire canopy cover data were originally derived from Landsat Thematic Mapper (TM) images (30 m × 30 m resolution) by LEMMA (2012; for Tripod and Toolbox locations) or the U.S. Forest Service Remote Sensing Application Center (Johnson et al. 2000; for Star Gulch).

In the field, we measured density and diameter of snags (height ≥ 1.4 m) associated with woodpecker nest sites and randomly located non-nest sites. We counted the number of large snags (dbh ≥ 23 cm; dbh = diameter at 1.4 m from ground) within 11.3-m–radius circular plots (0.04 ha) centered on nest and non-nest sites at Star

TABLE 2. Environmental variables considered in habitat suitability models for wildfire-associated woodpeckers. Data sources were either remotely sensed GIS layers (R) or field-collected measurements (F). Remotely sensed variables were calculated at any of 3 spatial scales: pixel = value from 30-m pixel, local = 0.81-ha moving window (3 × 3 cells), and landscape = 314-ha moving window (1-km–radius circle). Additionally, 2 variables describing the extent of logging were compiled for reference, but were not considered as modeling covariates.

Variable name (abbreviation)	Data source	Spatial scale(s)	Description (units, if any)
Slope (slp)	R	pixel	Topographic slope (% rise over run)
Sine aspect (sinasp)	R	pixel	Sine-transformed (east–west) orientation of slope
Cosine aspect (cosasp)	R	pixel	Cosine-transformed (north–south) orientation of slope
Burn severity (ΔNBR)	R	local	Median index of burn severity using Landsat TM satellite imagery for 1-ha moving window
Moderate canopy cover (LocCCmd[a], LndCCmd)	R	local, landscape	Proportion area with 40–70% canopy cover
High canopy cover (LndCChi)[b]	R	landscape	Proportion area with >70% canopy cover
Tree size (dbh)[c]	F	n/a	Diameter at breast height of the snag/tree (>1.4 m tall) containing the nest cavity or associated with a non-nest site (cm). Each non-nest dbh value represented a snag/tree selected randomly within 11.3 m of non-nest–site coordinates.
Snag density (snag)[c]	F	n/a	Number of large snags ≥1.4 m tall and ≥23 cm dbh within 11.3 m (0.04 ha) of nest cavities or nearest non-nest snag/tree
Logging (LocLog, LndLog)[d]	R	local, landscape	Proportion area within sale units treated with salvage logging

[a] Very few sites had any high canopy cover at the local scale, so we only considered proportion moderate canopy cover at this scale.
[b] Very little area was characterized by a high pre-fire canopy cover at the Toolbox location, so this variable was not considered in Toolbox models.
[c] Field-collected variables were only measured at Tripod and Star Gulch locations.
[d] Logging variables were not considered as model covariates, but were summarized to inform discussion.

Gulch and Tripod locations. We also measured dbh of each snag/tree occupied by a nesting woodpecker, and dbh of a randomly selected snag/tree within 11.3 m of each non-nest site to represent dbh of available trees (Table 2; for relevance, see Russell et al. 2007). At Toolbox, we counted snags within 2 perpendicular transects (100 m × 20 m; total area = 4,000 m^2) centered only on nest sites and only measured dbh of nest trees. We re-scaled all snag counts to the number per 0.04 ha for comparability across locations.

We quantified the extent of salvage logging (proportion area within logging sale units) at local and landscape scales (Table 2). Inclusion of these logging covariates did not improve model applicability. Furthermore, logging extent, intensity, and distribution varied among our locations such that we did not expect logging relationships quantified at one location to be transferable to other locations. We therefore excluded logging covariates from reported models. Although logging can affect woodpecker nest site selection and nesting densities (Saab et al. 2007, Saab et al. 2009), a minority (20–30%) of the landscape was affected by logging and model transferability for disturbance-associated woodpeckers is largely untested (but see Tingley et al. 2016). We therefore evaluated model transferability given available data in the interest of directing ongoing research, and we compiled summary statistics for logging covariates for reference and discussion (Appendix A).

Modeling Habitat Suitability

Model development and selection. We modeled habitat suitability from nest and non-nest sites as a function of remotely sensed covariates, or a combination of remotely sensed and field-collected covariates. We employed weighted logistic regression wherein we weighted observations of zeros (non-nest sites) to ones (nest sites) by their relative sample sizes ($w_1 = 1$; $w_0 = n_1/n_0$) to negate the influence of sample size on the estimated response variable (Russell et al. 2007, Saab et al. 2009). This weighting scheme recognizes the ratio of zeros to ones as an artifact of sampling with no biological significance. As such, estimated response probabilities are only interpretable as relative indices of habitat suitability (Russell et al. 2007; hereafter habitat suitability indices or HSIs). Ideally, zeros should represent unused locations that are not contaminated with misclassified nesting locations (Keating and Cherry 2004). Our field methods resulted in a thorough search of study units, so we are reasonably confident that non-nest sites were never used for nesting during the study period. We fitted weighted logistic regression models using the glm function in R (v. 3; R Core Team 2015). Habitat suitability indices primarily quantified relative suitability for nest site selection but could also reflect nest predation and competition because some nests were found after initiation. Nest site selection, predation, and competition all contribute to nesting habitat suitability and potentially influence woodpecker distributions.

To generate models with maximum predictive ability for guiding management decisions, we considered models that exhausted potential covariate combinations with restrictions on model complexity based on sample size (see also Russell et al. 2007). We limited the number of covariate parameters in a model (not including the intercept) to one-tenth the number of nests in the analyzed sample. We only considered additive combinations of linear covariate relationships to limit model complexity and because no strong biological rationale existed for any particular nonlinear (e.g., quadratic or interactive) relationships. Nonlinear relationships could arise if woodpeckers select for specific ranges of burn severity, canopy cover, or snag densities and diameters, or if selection patterns vary with habitat availability (e.g., Aarts et al. 2013). Nevertheless, we found no improvements to model transferability when we considered nonlinear relationships (Appendix B). We therefore focused the remainder of this paper on additive linear models.

We selected a model for each woodpecker species from all subsets of either (1) only remotely sensed covariates (remotely sensed models) or (2) both remotely sensed and field-collected covariates (combination models) at each wildfire location where data were available. Because Lewis's Woodpeckers did not occur at the Tripod location and field-collected data were not available at Toolbox, we constructed 8 model sets (both species, all locations) and selected one model from each set: 3 remotely sensed and 2 combination sets for Black-backed Woodpecker, and 2 remotely sensed and 1 combination sets for Lewis's Woodpecker. We evaluated transferability for a model selected from each set with the lowest Akaike's Information Criterion value corrected for small sample size (AIC_c; Burnham and Anderson 2002). We evaluated predictions from individual models rather than model-averaged predictions because the former is easier to interpret, and because we expected selected models to adequately represent plausible models for evaluating transferability across locations.

Evaluating model transferability. For each model developed at a given wildfire location (development locations; described above), we evaluated transferability by applying the model and measuring discrimination of nest from non-nest sites at alternate locations (application locations). We considered a model transferable if it discriminated nest from non-nest sites at both development and application locations as measured by the criteria described hereafter.

Although numerous methods have been developed for evaluating predictive models (Fielding and Bell 1997, Pearce and Ferrier 2000, Jiménez-Valverde 2012), correct discrimination of suitable versus unsuitable nesting habitat was our priority to inform habitat management for sensitive woodpecker species. We therefore evaluated transferability primarily in terms of model discrimination of nest and non-nest sites. We used receiver-operating curves (ROC) and area under these curves (AUC) to evaluate discrimination (Fielding and Bell 1997). An AUC $= 0.5$ indicates discrimination that is no better than random and AUC $= 1$ indicates perfect discrimination (Fielding and Bell 1997, Pearce and Ferrier 2000), but if sampling is evenly distributed over HSI values, an ideally calibrated model yields an AUC $= 0.83$ (Jiménez-Valverde et al. 2013). We therefore considered AUC $\gtrsim 0.8$ indicative of strong performance and lower AUC values indicative of poorer performance. To provide additional information for understanding model performance, we generated density plots comparing smoothed histograms of HSI values for nest and non-nest sites (see also Russell et al. 2007).

To further inform model application, we evaluated the transferability of HSI thresholds for discriminating suitable versus unsuitable nesting habitat (see Jiménez-Valverde and Lobo 2007, Liu et al. 2013). For any given threshold, sensitivity is the percentage of used (nest) sites correctly classified suitable (HSI $>$ threshold), and specificity is the percent unused (non-nest) sites classified unsuitable. Thresholds can be selected based on various criteria (Jiménez-Valverde and Lobo 2007, Liu et al. 2013), but regardless should consistently discriminate used from unused sites across locations to be transferable. Different management objectives may call for thresholds that variously balance sensitivity versus specificity, but we expect managers will typically want thresholds that classify a majority of nest sites suitable (i.e. sensitivity > 0.5). We therefore considered a range of thresholds associated with sensitivities $\approx$ 0.90, 0.75, and 0.60 at development locations for each model. We evaluated transferability of these thresholds in terms of whether they discriminated habitat well at development locations and maintained discriminative utility at application locations. We considered thresholds useful if they classified a large majority of nest sites as suitable (sensitivity $\gtrsim 60\%$) while classifying a substantial portion of non-nest sites as unsuitable (specificity $\gtrsim$ 30%).

TABLE 3. Summary of model selection results. Models describe Black-backed Woodpecker (BBWO) and Lewis's Woodpecker (LEWO) nest site selection at Star Gulch (SG), Toolbox (TB), or Tripod (TP) wildfire locations using either remotely sensed variables only (R) or a combination of remotely sensed and field-collected variables (C). The table reports the number of models considered, the number of models within 2 AIC_c units of the top model (plausible models), and the ΔAIC_c for a model without any covariates (intercept-only model).

Species	Location	Potential covariates	Number of models considered	Number of plausible models	Intercept-only ΔAIC_c
BBWO	SG	R	99	9	7.60
		C	256	1	35.69
	TB	R	63	4	35.54
	TP	R	64	5	20.37
		C	130	2	31.81
LEWO	SG	R	120	6	26.30
		C	382	3	73.48
	TB	R	63	3	12.73

RESULTS

Field Summary

We measured 28–249 Black-backed Woodpecker nest sites at each of 3 study locations, and 47 and 50 Lewis's Woodpecker nest sites at each of 2 locations, along with comparable samples of non-nest sites (Table 1). A wide range of conditions was available for nesting (represented by non-nest sites), although wildfire locations differed in the range of environmental conditions (Appendix A). Broadly, Tripod and Star Gulch locations were characterized by more topography than at Toolbox, Toolbox was burned more severely and Tripod less severely than Star Gulch, pre-fire canopy cover tended to be more moderate at Toolbox and higher at Tripod compared to Star Gulch, and Star Gulch had larger-diameter snags at higher densities than did Tripod. Logging affected ~20% of sampled areas centered on Toolbox non-nest sites and ~30% of sampled areas at Star Gulch non-nest sites (Appendix A).

Model Selection

All selected models improved upon intercept-only models by $\geq$ 11.22 AIC_c units (Table 3 and Appendix C), and all included statistically supported covariate relationships, indicating significant habitat differences between nest and non-nest sites at each location (Tables 4 and 5). All selected models included statistically supported positive relationships with variables reflecting burn severity: ΔNBR, snag density, or both. Selected models with field-collected covariates also consistently described positive relationships with tree diameter for both woodpecker species. Selected models described relationships with pre-fire canopy cover, but the direction of these relationships varied among locations and woodpecker species, and salvage logging extent. For Black-backed Woodpeckers, relationships with

TABLE 4. Maximum likelihood parameter estimates (SE) for selected habitat suitability models for nesting Black-backed Woodpeckers at 3 wildfire locations. Models selected were those with the lowest AIC_c value from each model set. Covariates considered were either only remotely sensed (remote) or a combination of remotely sensed and field collected (combination). Only parameters appearing in at least one selected model are represented.

	Star Gulch		Toolbox	Tripod	
Parameter	Remote	Combination	Remote	Remote	Combination
Intercept	−4.2 (1.6)	−12.4 (3.4)	−0.77 (0.2)	−6.3 (2.5)	−5.6 (1.5)
Slope	–	–	−0.037 (0.010)[a]	–	–
Sine aspect	–	–	0.31 (0.14)[a]	–	–
Cosine aspect	–	1.3 (0.6)[a]	–	–	–
Burn severity (ΔNBR)	0.004 (0.001)[a]	–	0.002 (0.0005)[a]	0.006 (0.002)[a]	0.006 (0.002)[a]
Canopy cover:					
Landscape moderate	6.0 (3.2)	14.4 (5.7)[a]	–	6.8 (4.1)	–
Tree size (dbh)	–	0.14 (0.03)[a]	–	–	0.09 (0.04)[a]
Snag density	–	0.16 (0.06)[a]	–	–	0.18 (0.1)

[a] Covariate slope parameter estimates whose 95% CIs do not overlap zero.

TABLE 5. Maximum-likelihood parameter estimates (and SEs) for habitat suitability models for nesting Lewis's Woodpeckers at 2 wildfire locations. Models selected were those with the lowest AIC_c value from each model set. Covariates considered were either only remotely sensed (remote) or a combination of remotely sensed and field collected (combination). Only parameters appearing in at least one selected model are represented.

	Star Gulch		Toolbox
Parameter	Remote	Combination	Remote
Intercept	−7.5 (1.8)	−18.4 (4.1)	0.5 (1.1)
Sine aspect	0.87 (0.40)[a]	–	–
Cosine aspect	–	1.54 (0.64)[a]	–
Burn severity (ΔNBR)	0.005 (0.001)[a]	0.004 (0.002)	0.003 (0.001)[a]
Canopy cover:			
Local moderate	–	–	–
Landscape moderate	11.5 (3.3)[a]	19.1 (6.1)[a]	−4.3 (1.6)[a]
Tree size (dbh)	–	0.16 (0.04)[a]	–
Snag density	–	0.15 (0.06)[a]	–

[a] Covariate slope parameter estimates whose 95% CIs do not overlap zero.

pre-fire canopy cover only appeared in 3 of 5 selected models, but these 3 models consistently described positive relationships with moderate landscape-scale pre-fire canopy cover. For Lewis's Woodpecker, Star Gulch models described significantly positive relationships with moderate pre-fire canopy cover (landscape scale), but the Toolbox model described significantly negative relationships with this feature (both spatial scales). For Black-backed Woodpeckers, only the Toolbox model described relationships with topography (i.e. a negative relationship with slope and a positive relationship with east-facing aspect). For Lewis's Woodpecker, models described relationships with aspect that varied among locations and models.

Predictive Performance and Transferability

When evaluated with the same data used for model development, models discriminated nest from non-nest sites at development locations relatively well (AUC = 0.660–0.951; see diagonal elements in Figures 2–5). In contrast, discrimination was poorer and more variable at application locations (AUC = 0.430–0.873; off-diagonal elements in Figures 2–4). Consistent with AUC-based results, classification thresholds were useful for discriminating nest from non-nest sites at development locations but often less useful when transferred to application locations (Table 6).

For Black-backed Woodpeckers, none of the remotely sensed models were consistently transferable across all 3 wildfire locations (Table 6, Figure 2; for density plots, see Appendix Figure 6 in Appendix D). Remotely sensed models developed at Star Gulch and Tripod locations showed moderate to strong discrimination of nest from non-nest sites where developed and applied within these 2 locations (AUC ≥ 0.713; Figure 2 and Appendix Figure 6). Thresholds for the Star Gulch model were also useful for discrimination when applied at Tripod (sensitivity ≥ 92%, specificity ≥ 38%). Tripod thresholds classified only a small majority of Star Gulch nest sites as suitable, however (sensitivity ≤ 58%; Table 6), reflecting assignment of lower HSIs to Star Gulch nest sites (Appendix Figure 6). Additionally, both models and associated thresholds discriminated nest versus non-nest sites poorly at Toolbox (Table 6, Figure 2 and Appendix Figure 6). Interestingly, the Toolbox remotely sensed model was more discriminating when applied at Tripod (AUC = 0.782) compared to Toolbox where it was developed (AUC = 0.66; Figure 2). Nevertheless, this model assigned low HSIs to nest sites (Appendix Figure 6) and thresholds were consequently less useful at Tripod (sensitivity ≤ 15%), and the model showed poor discrimination in general at Star Gulch (AUC = 0.559, Figure 2 and Appendix Figure 6; sensitivity ≤ 28%, Table 6).

Combination models for Black-backed Woodpeckers exhibited better but not necessarily universal transferability. When transferred between Star Gulch and Tripod locations, these models consistently discriminated nest from non-nest sites at both locations (AUC ≥ 0.83; Figure 3; for density plots, see Appendix Figure 7 in Appendix D). Additionally, all 3 thresholds for each model classified most nest sites as suitable (sensitivity ≥ 62%) while classifying many non-nest sites unsuitable (specificity ≥ 26%; Table 6). Nevertheless, this model assigned low HSIs to many Toolbox nest sites (Appendix Figure 7) so only one threshold for each combination model classified ≥ 60% of Toolbox nest sites suitable, suggesting poor transferability to the Toolbox location (Table 6).

Remotely sensed models for Lewis's Woodpeckers exhibited poor transferability. Both models discriminated nest from non-nest sites well at development locations (sensitivity ≥ 60%, specificity ≥ 43%, AUC ≥ 0.728; Table 6, Figure 4; for density plots, see Appendix Figure 8 in Appendix D). At application locations, however, discrimination of nest versus non-nest sites was much poorer (AUC

TABLE 6. HSI thresholds for classifying suitable habitat and their performance. Thresholds classify habitat for nesting Black-backed Woodpeckers (BBWO) and Lewis's Woodpeckers (LEWO). Models were developed using nest and non-nest sites at each of 3 wildfire locations (Star Gulch [SG], Toolbox [TB], and Tripod [TP]) and applied across locations. Classification thresholds were selected to approximate sensitivity (percent nest sites classified as suitable) at 3 desired levels (60%, 75%, and 90%) at the development location. Percentages of non-nest sites identified unsuitable (specificity) are also reported. Models included either remotely sensed covariates only (R) or a combination of remotely sensed and field-collected covariates (C). Sensitivity and specificity are presented at development and application locations to assess transferability.

		Development location		Application location	
Model: species, location, covariates	Classification threshold	% nests identified	% non-nests identified	% nests identified	% non-nests identified
BBWO, SG, C	0.77	61	98	TB:38; TP:62	TP:94
	0.66	75	89	TB:50; TP:65	TP:90
	0.28	92	68	TB:76; TP:85	TP:75
BBWO, SG, R	0.53	61	66	TB:88; TP:92	TB:18; TP:69
	0.45	75	55	TB:92; TP:96	TB:7; TP:53
	0.35	92	38	TB:95; TP:96	TB:2; TP:38
BBWO, TB, R	0.51	60	61	SG:11; TP:0	SG:96; TP:100
	0.45	75	48	SG:22; TP:4	SG:91; TP:97
	0.38	90	32	SG:28; TP:15	SG:77; TP:97
BBWO, TP, C	0.88	62	97	TB:29; TP:62	SG:72
	0.76	77	91	TB:53; TP:77	SG:57
	0.28	92	74	TB:92; TP:92	SG:26
BBWO, TP, R	0.72	62	88	SG:25; TB:49	SG:98; TB:61
	0.46	77	74	SG:47; TB:76	SG:72; TB:37
	0.36	92	71	SG:58; TB:87	SG:66; TB:21
LEWO, SG, C	0.93	60	100	TB:70	no data
	0.83	76	100	TB:72	no data
	0.31	90	77	TB:85	no data
LEWO, SG, R	0.64	60	85	TB:62	TB:31
	0.53	78	74	TB:62	TB:21
	0.28	90	43	TB:70	TB:8
LEWO, TB, R	0.55	62	72	SG:54	SG:55
	0.42	77	51	SG:78	SG:32
	0.30	91	35	SG:96	SG:15

$\leq$ 0.573; Figure 4). Additionally, 3 thresholds classified $\leq$ 21% non-nest sites as unsuitable (Table 6) because HSIs for non-nest sites were higher at application locations. Finally, one threshold for the Toolbox model classified only 54% of Star Gulch nest sites suitable (Table 6).

The combination model and associated classification thresholds for Lewis's Woodpeckers was strongly discriminating at Star Gulch where the model was developed (Table 6, Figure 5; for density plot, see Appendix Figure 9 in Appendix D). Furthermore, this model assigned similar HSIs to Toolbox nest sites (Appendix Figure 9), so a similar percent of Toolbox nest sites was classified suitable, suggesting possible transferability from Star Gulch to Toolbox (Table 6). We lacked the necessary non-nest data at Toolbox, however, to fully evaluate transferability between these locations.

DISCUSSION

We found variable transferability of habitat suitability models developed at individual wildfire locations to other locations, suggesting limited generality of such models throughout the range of our study species. Models developed with only remotely sensed covariates were partially transferable across locations for Black-backed Woodpecker, but consistently showed poor transferability for Lewis's Woodpecker. Models that combined remotely sensed and field data for Black-backed Woodpecker performed better at the 2 locations where nest and non-nest field data were collected. These models characterized many Toolbox nest sites as unsuitable, however, suggesting potentially restricted applicability to other locations. The combination model for Lewis's Woodpeckers classified desirably large percentages of Toolbox nests as suitable, suggesting possible transferability, but without non-nest field measurements at application locations, our evaluation of this model was limited. As expected, models that included field-collected covariates performed better than models with only remotely sensed covariates (see also Russell et al. 2007).

We also evaluated several HSI-based thresholds for each model to support various management objectives that

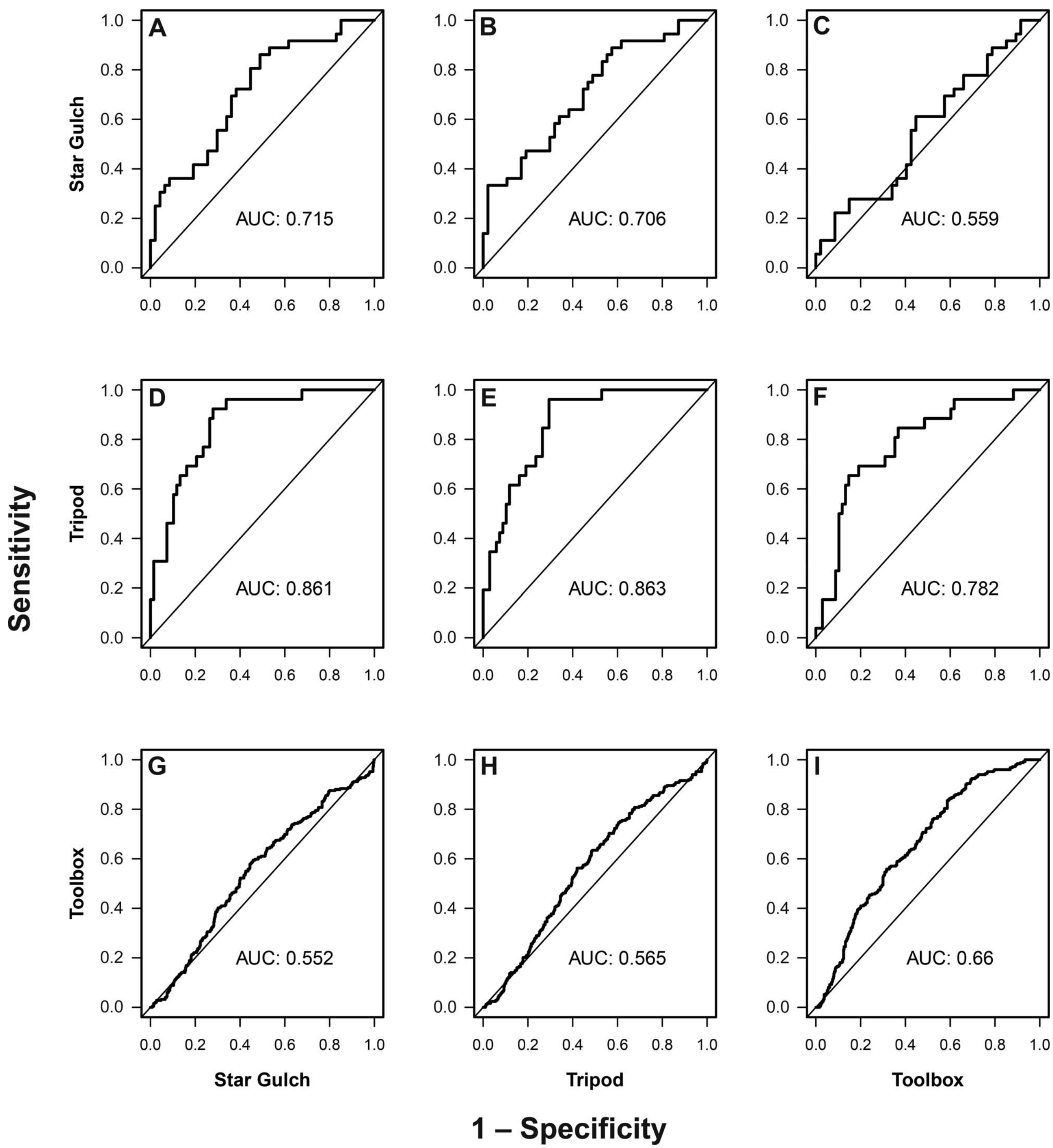

FIGURE 2. Black-backed Woodpecker receiver-operating curves for remotely sensed models. Receiver-operating curves and area under these curves (AUC) for habitat suitability models for Black-backed Woodpeckers with only remotely sensed covariates. Discrimination of nest versus non-nest sites is assessed by plotting sensitivity (the proportion of nest sites correctly classified) against 1 − specificity (the proportion of non-nest sites misclassified). Discriminatory performance is assessed for locations where models were developed (**A**, **E**, **I**) and where they were applied to assess transferability (**B**, **C**, **D**, **F**, **G**, **H**).

require categorization of sites based on suitability (e.g., as suitable versus unsuitable). Managers with objectives that require liberal estimates of habitat can use lower thresholds, which will designate more nest sites but also more unused sites as suitable habitat. Conversely, managers can use higher thresholds to meet objectives requiring conservative estimates of habitat. Regardless, thresholds should perform consistently across locations in how well

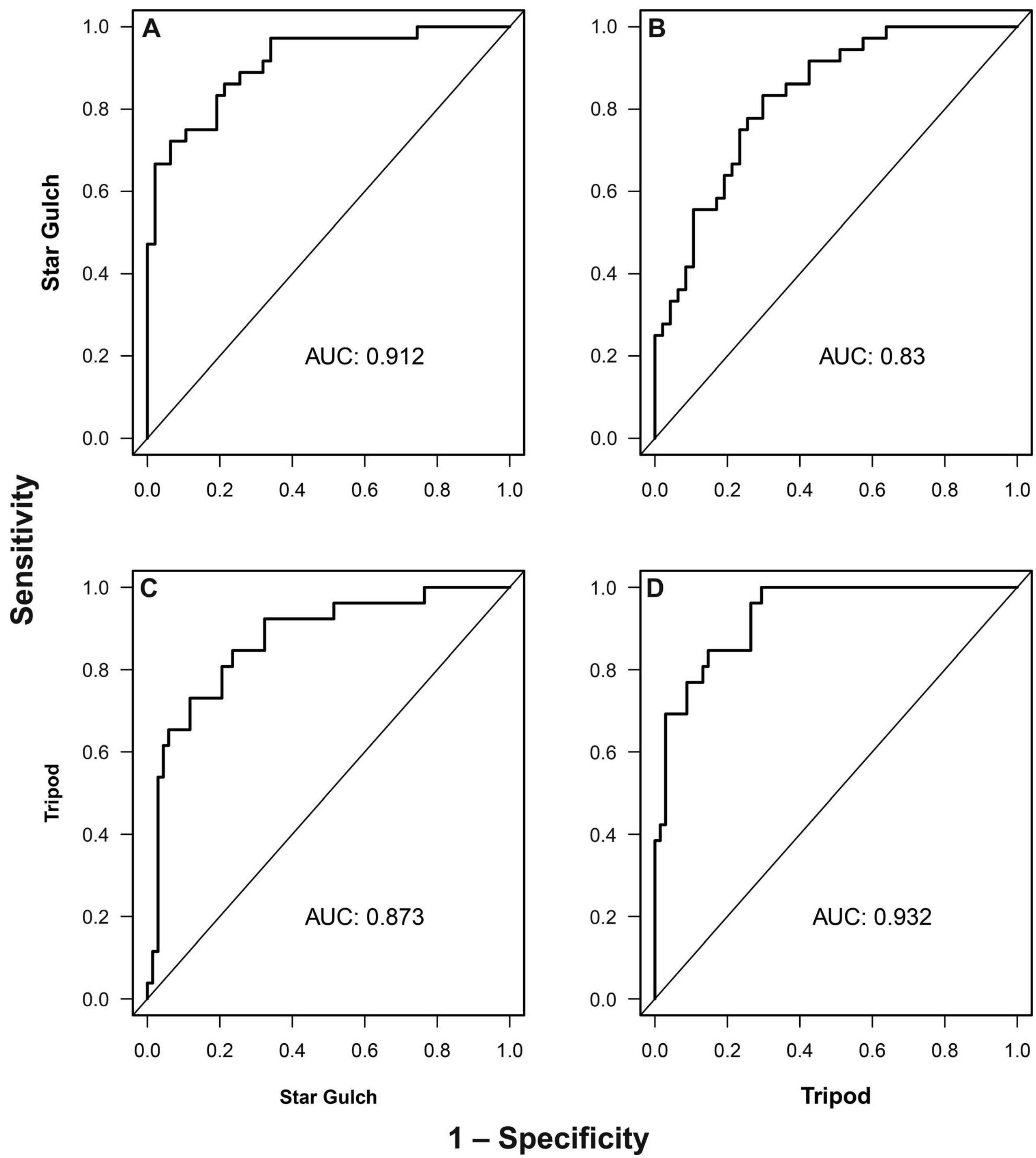

FIGURE 3. Black-backed Woodpecker receiver-operating curves for combination models. Receiver-operating curves and area under these curves (AUC) for habitat suitability models for Black-backed Woodpeckers with remotely sensed and field-collected covariates. Discrimination of nest versus non-nest sites is assessed by plotting sensitivity (the proportion of nest sites correctly classified) against 1 − specificity (the proportion of non-nest sites misclassified). Discriminatory performance is assessed for locations where models were developed (**A**, **D**) and where they were applied to assess transferability (**B**, **C**).

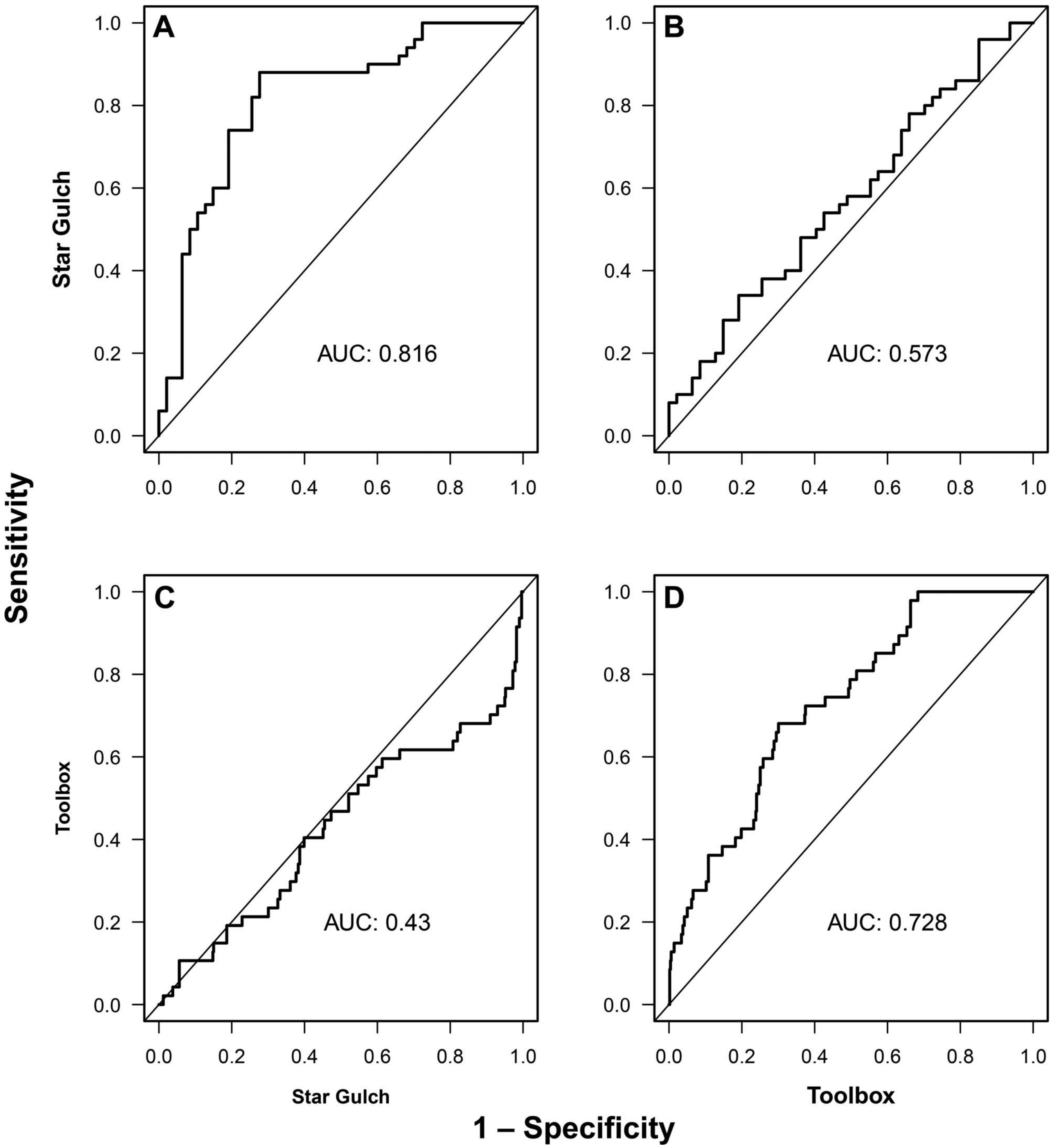

FIGURE 4. Lewis's Woodpecker receiver-operating curves for remotely sensed models. Receiver-operating curves and area under these curves (AUC) for habitat suitability models for Lewis's Woodpeckers with only remotely sensed covariates. Discrimination of nest versus non-nest sites is assessed by plotting sensitivity (the proportion of nest sites correctly classified) against 1 − specificity (the proportion of non-nest sites misclassified). Discriminatory performance is assessed for locations where models were developed (**A**, **D**) and where they were applied to assess transferability (**B**, **C**).

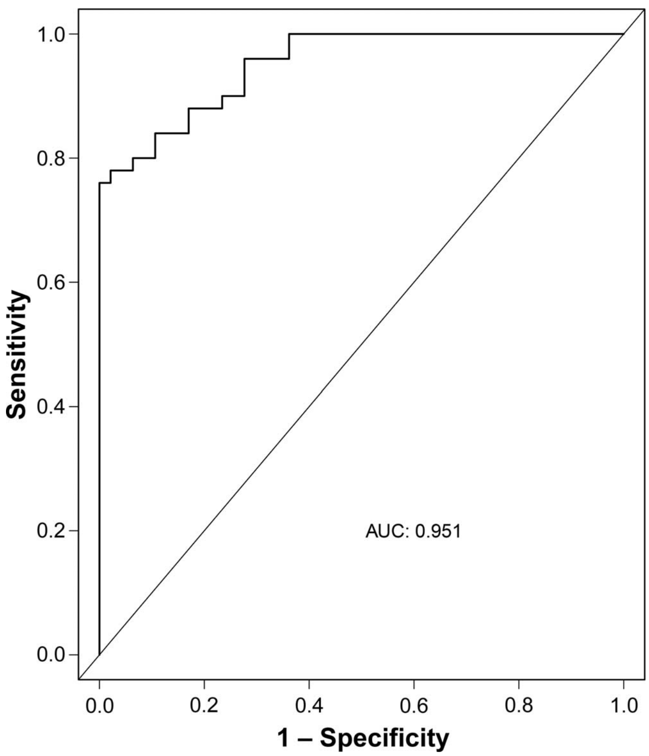

FIGURE 5. Lewis's Woodpecker receiver-operating curve for combination model. Receiver-operating curve and area under this curve (AUC) for a habitat suitability model for Lewis's Woodpeckers with remotely sensed and field-collected covariates developed and applied at the Star Gulch wildfire location (Idaho). Discrimination of nest versus non-nest sites is assessed by plotting sensitivity (the proportion of nest sites correctly classified) against 1 − specificity (the proportion of non-nest sites misclassified).

they discriminate nest from non-nest sites for general applicability. Our results indicate limited transferability of thresholds, largely paralleling that of continuous HSIs.

Factors Affecting Model Transferability

To be transferable, models should describe biologically meaningful environmental relationships that generally determine species distributions while avoiding location-specific relationships that are not generalizable (Guisan and Thuiller 2005). Relationships with some habitat features were consistent across locations, likely allowing the limited transferability that we observed (e.g., mainly between Star Gulch and Tripod locations). We consistently observed positive relationships with burn severity for both woodpecker species across locations, likely reflecting fundamental associations with burned forests and the resources provided therein (Saab et al. 2009, Latif et al. 2013, Tingley et al. 2014). Nest cavities were consistently located in relatively large snags because they provide desirable structure and thermal properties for excavation and clutch rearing (e.g., Bull et al. 1997). Positive relationships for Black-backed Woodpeckers with field-measured snag densities and moderate-to-high remotely sensed pre-fire canopy cover (i.e. where snag densities were likely relatively high) were also consistent across locations and with known habitat associations (Saab et al. 2009, Latif et al. 2013, Tingley et al. 2014).

Relationships with other features that varied among locations likely limited model transferability. Lewis's Woodpeckers favor relatively open areas with low snag densities (e.g., Saab et al. 2009, Vierling et al. 2013); the negative relationship with moderate pre-fire canopy cover (implying a positive relationship with low pre-fire canopy cover) quantified at Toolbox was consistent with this affinity. Star Gulch models, however, were counterintuitive because of positive relationships with moderate pre-fire canopy cover and snag density. Logging occurred during 3 of 4 years of the sampling period at Toolbox, whereas logging at Star Gulch occurred during the first year of sampling. The timing and distribution of logging relative to sampling may affect how pre-fire canopy relates with snag densities and thus nest site selection. For Lewis's Woodpecker, the largest snags (>50 cm dbh) are particularly important for nesting and shrub cover is a key component of desirable foraging habitat (Saab et al. 2009, Newlon and Saab 2011, Vierling et al. 2013). Inadequate quantification of relationships with these features, particularly by models with only remotely sensed covariates, may explain poor model transferability for this species. Estimated relationships with topography also varied among locations for both woodpecker species, suggesting limited generality of how nest site selection relates with topography.

Varying resource selection patterns can arise from differences in habitat available at different locations (Aarts et al. 2013). Models exhibited the least transferability between Toolbox and the other 2 locations. Less slope, lower snag densities, varying snag diameters, and greater tree species richness (Appendix A; Hollenbeck et al. 2013) likely influenced different selection patterns at Toolbox compared to other locations, suggesting relationships may vary among forest types.

Although we excluded logging covariates from our models for reasons described above, logging occurred most extensively at the Toolbox location (within and surrounding sampling units), followed by the Star Gulch location (outside study units only), and logging was negligible at the Tripod location. Salvage logging could have hindered model transferability. Salvage logging can affect how habitat selection relates with other aspects of the environment (Saab et al. 2009), either by changing the range of conditions available (sensu Aarts et al. 2013; e.g., could explain differential selection for snag density) or by changing the distribution of resources (e.g., by favoring flat areas, logging may alter how snag densities relate with topography). Additionally, salvage logging may have altered the utility of remotely sensed pre-fire canopy covariates. We expected these covariates to index post-fire snag density (cf. Russell et al. 2007), but salvage logging may have disrupted this relationship.

Limitations on continuous HSIs also apply to transferability of HSI-based classification thresholds. In some cases, however, continuous HSIs transferred better than corresponding thresholds (e.g., the Black-backed Woodpecker remotely sensed model developed at Tripod). In these cases, nest sites were consistently assigned higher HSIs than non-nest sites, but HSI values also varied among locations, altering how well particular thresholds classify habitat. Even if selection patterns are consistent across locations (e.g., nest placement always favors relatively high-severity burned sites), the range of available conditions may constrain the expression of selectivity at some locations more than others. Additionally, local abundance can influence threshold performance (Manel et al. 2001). Observed nesting densities varied among our study locations (see Table 1), but this variation did not appear to overwhelm threshold transferability (i.e. sensitivities and specificities in Table 6 did not consistently relate with nest densities as described by Manel et al. 2001). Regardless, even with generally applicable HSI models, additional factors can influence threshold transferability, so thresholds should ideally be evaluated with independent data prior to their widespread application.

Broader Implications and Future Directions

Several previous efforts developed habitat models to inform post-fire habitat management for woodpeckers and other cavity-nesting species (Russell et al. 2007, Saab et al. 2009, Wightman et al. 2010, Saracco et al. 2011, Tingley et al. 2016). Transferability of these models has not been widely tested, however, so their generality remains uncertain (but see Tingley et al. 2016). Our results suggest data from any one wildfire location are unlikely to support predictive modeling for nesting Lewis's or Black-backed woodpeckers at novel locations. Individual wildfire locations represented a limited range of available habitats encountered across the range of these species, which is commonly a challenge when quantifying habitat selection patterns and species distributions (Morrison 2012, Aarts et al. 2013). Thus, data from multiple locations are likely needed to develop broadly applicable predictive models (e.g., Latif et al. 2013).

Having acquired more extensive data, various approaches could improve model transferability and generality. Our results suggest habitat selection patterns vary among locations possibly due to variation in habitat availability or in natural selection pressures (e.g., location-specific variation in competitor or predator species). Simple linear models will therefore likely be limited for generally quantifying habitat suitability patterns even with more extensive data (Morrison 2012, Aarts et al. 2013). Models with nonlinear or interactive relationships could quantify spatially varying habitat selection patterns (e.g., Aarts et al. 2013). Alternatively, separate models could quantify region-specific habitat relationships and distributions (Preston et al. 2008, DeCesare et al. 2012). Combining predictions from multiple models using ensemble approaches could also be valuable (Araújo and New 2007, Latif et al. 2013), but evaluation with independent data would be necessary to assess transferability.

Combining different types of data collected across different spatial scales corresponding with different levels of habitat selection could be beneficial (e.g., DeCesare et al. 2012). For Black-backed Woodpeckers, model-based home range size predictions combined with occupancy probabilities estimated across wildfire locations have provided broadly applicable estimates of abundance (Tingley et al. 2016).

Numerous model selection approaches exist and vary in their propensity for identifying predictive models (Johnson and Omland 2004, Hooten and Hobbs 2015). We took the relatively common approach of selecting the top model ranked by AIC_c, but this approach may not identify the most predictive model (Barbieri and Berger 2004). A more direct approach may be to explicitly select models based on predictive performance at application locations using cross-validation (Wiens et al. 2008).

To effectively inform post-fire habitat management, we need to account for salvage logging when developing predictive habitat models. One approach would be to restrict model development to unlogged landscapes for at least 5 years after wildfire to obtain sufficiently large datasets to support predictive modeling of nesting woodpeckers (e.g., Russell et al. 2007). This approach would provide readily interpretable predictions that are most reliable for mapping habitat to inform reserve design. Salvage logging, however, typically occurs within the first 2 years after wildfire in dry conifer forests because the economic value of burned timber declines quickly with time since fire. Additionally, much of the funding for post-fire wildlife surveys arises from an interest in monitoring salvage logging (Saab et al. 2009). Thus, opportunities for surveying unlogged burned forests are limited. An alternative approach could involve applying salvage logging strategically to extend the range of environmental conditions sampled, specifically across the distributions of snag densities and diameters, and size and configuration of retained snag patches. More surveys would likely be needed, however, to adequately sample an extended environmental range. Additionally, tracking environmental attributes affected by salvage logging (i.e. tree species, snag densities and diameters, and patch attributes) would be necessary. Such information typically requires field measurements, which limit predictive habitat mapping. Improved resolution of remotely sensed data (e.g., LiDAR) over large landscapes could provide the fine resolution data needed to relax this limitation (Recio et al. 2013), although model applicability would still be restricted to locations where such data are available.

Models developed here quantify nesting habitat for both species strictly during the early post-fire period. Black-backed Woodpecker nesting densities peak within the first 5 years whereas Lewis's Woodpecker densities increase for $\geq$ 10 years following wildfire (Saab et al. 2007). Lewis's Woodpecker distributions during mid-to-late post-fire periods will likely shift as post-fire ecological succession progresses in ways that to our knowledge have not been explicitly quantified.

Management Implications

Forest managers are challenged with meeting socioeconomic demands for salvage logging along with mandates requiring habitat conservation for disturbance-associated woodpeckers. Predictive habitat suitability models can offer rigorous data-driven information for post-fire forest management planning and decisions, but broadly applicable models are needed. Such models would most likely require data from multiple wildfire locations to represent an adequate range of environmental conditions. Salvage logging could be used to broaden the environmental conditions sampled at individual locations, but doing so would likely require additional survey effort and high-resolution environmental data (e.g., LiDAR or field-collected measurements).

Ensemble predictions from models that combine data from the 3 locations studied here have been developed for Black-backed Woodpecker (Latif et al. 2013). Transferability of these predictions to new wildfire locations, however, has not been evaluated. Additionally, these predictions are too coarse to inform design of logging prescriptions because of their reliance on remotely sensed data. Lewis's Woodpecker (studied here) and White-headed Woodpecker (Wightman et al. 2010) provide important complements to Black-backed Woodpecker as reference species to inform post-fire forest management (Saab et al. 2007, Saab et al. 2009). Further development and evaluation of predictive models for all 3 species would therefore be highly desirable.

Although limited in applicability, models reported here may be locally applicable to locations similar to where models were developed. Additionally, models presented here do reflect key habitat components and describe at least a subset of environmental conditions suitable for and selected by nesting Black-backed and Lewis's woodpeckers. Thus, data reported here and elsewhere (Russell et al. 2007, Saab et al. 2009, Wightman et al. 2010, Saab et al. 2011) represent important baseline information to guide further sampling and possibly inform salvage logging particularly if coupled with research to inform adaptive habitat management.

Because Black-backed and Lewis's woodpeckers favor different conditions for nesting, managers can target these species (along with White-headed Woodpeckers; Wightman et al. 2010) to guide conservation of a range of habitat conditions generated by wildfire. That range of conditions will likely provide habitat for other cavity-dwelling vertebrates (Saab et al. 2007, 2009). Ongoing research developing and evaluating habitat suitability models for disturbance-associated woodpeckers provides information and tools necessary for forest managers to meet conservation objectives for multiple species.

ACKNOWLEDGMENTS

We thank location managers C. Forristal and A. Markus in Oregon and K. Woodruff in Washington for overseeing data collection. We are grateful to the many field assistants who worked long, hot, wet, and cold days to collect the field data. R. Russell and K. Podrozny contributed substantially in initial phases of the study and analysis. M. Tingley and J. Hagar provided thoughtful comments on initial versions of this manuscript.

Funding statement: This study was funded by the Joint Fire Science Program (#01-1-3-25 and #06-3-4-15), National Fire Plan (02.RMS.C.2), and the USDA Forest Service Rocky Mountain Research Station, Boise National Forest, Fremont-Winema National Forest, Okanogan-Wenatchee National Forest, and Pacific Northwest and Intermountain Regions.

Author contributions: Q.S.L. analyzed the data and wrote the paper. V.A.S. conceived the idea, designed survey protocols, supervised research at all stages, and substantially edited the paper. J.P.H. analyzed the data and provided editorial input. J.G.D. designed survey protocols, supervised data collection, managed data storage and compilation, and provided editorial input.

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APPENDIX A. Descriptive statistics for covariates at nest and random sites sampling 3 wildfire locations where habitat suitability models were developed for nesting Black-backed and Lewis's woodpeckers.

APPENDIX A TABLE 7. Descriptive statistics for model covariates at the Star Gulch wildfire location, Idaho. Models were developed for Black-backed and Lewis's woodpeckers (BBWO and LEWO, respectively). See Table 1 for variable descriptions and units.

		Mean (SD)		
Variable	Scale	BBWO	LEWO	Non-nest
Slope	pixel	38 (13)	34 (11)	34 (15)
Sine aspect	pixel	0.18 (0.69)	0.41 (0.53)	0.19 (0.68)
Cosine aspect	pixel	0.14 (0.71)	−0.02 (0.76)	−0.18 (0.7)
Burn severity (ΔNBR)	local	519.5 (210.2)	527.2 (205.4)	386.2 (179.4)
Moderate canopy cover	local	0.57 (0.32)	0.57 (0.34)	0.42 (0.36)
	landscape	0.43 (0.07)	0.45 (0.07)	0.40 (0.10)
High canopy cover	landscape	0.11 (0.06)	0.07 (0.05)	0.09 (0.06)
Tree size (dbh)	field	41 (12)	51 (16)	26 (17)
Snag density	field	12.33 (6.20)	11.02 (5.88)	7.87 (6.81)
Logging[a]	local	0.17 (0.36)	0.10 (0.28)	0.01 (0.05)
	landscape	0.27 (0.27)	0.21 (0.22)	0.33 (0.20)

[a] Logging variables not considered as modeling covariates but provided here for reference.

APPENDIX A TABLE 8. Descriptive statistics for model covariates at the Toolbox wildfire location, Oregon. Models were developed for Black-backed and Lewis's woodpeckers (BBWO and LEWO, respectively). See Table 1 for variable descriptions and units.

		Mean (SD)		
Variable	Scale	BBWO	LEWO	Non-nest
Slope	pixel	11 (9)	13 (8)	14 (12)
Sine aspect	pixel	0.05 (0.73)	−0.14 (0.74)	−0.15 (0.68)
Cosine aspect	pixel	0.18 (0.66)	0.11 (0.67)	0.17 (0.69)
Burn severity (ΔNBR)	local	532.7 (163.2)	564.6 (127.4)	467.6 (201.5)
Moderate canopy cover	local	0.75 (0.36)	0.63 (0.41)	0.73 (0.38)
	landscape	0.55 (0.13)	0.47 (0.18)	0.58 (0.11)
High canopy cover	landscape	0.02 (0.03)	0.02 (0.03)	0.02 (0.03)
Tree size (dbh)	field	30 (11)	69 (19)	n/a[a]
Snag density	field	4.44 (2.36)	3.31 (1.73)	n/a[a]
Logging[b]	local	0.19 (0.35)	0.27 (0.38)	0.23 (0.39)
	landscape	0.20 (0.19)	0.26 (0.19)	0.21 (0.22)

[a] Non-nest field-collected data were not available for this study at the Toolbox location.
[b] Logging variables not considered as modeling covariates but provided here for reference.

APPENDIX A TABLE 9. Descriptive statistics for model covariates at the Tripod wildfire location, Washington. Models were only developed for Black-backed Woodpeckers (BBWO) at this site. See Table 1 for variable descriptions and units.

		Mean (SD)	
Variable	Scale	BBWO	Non-nest
Slope	pixel	45 (12)	44 (11)
Sine aspect	pixel	−0.53 (0.68)	−0.53 (0.46)
Cosine aspect	pixel	0.32 (0.43)	0.2 (0.69)
Burn severity (ΔNBR)	local	567.1 (197.1)	257.2 (220)
Moderate canopy cover	local	0.47 (0.38)	0.56 (0.36)
	landscape	0.57 (0.1)	0.51 (0.09)
High canopy cover	landscape	0.22 (0.14)	0.19 (0.13)
Tree size (dbh)	field	31 (16)	15 (14)
Snag density	field	7.9 (5)	2.6 (3.2)
Logging	local	0.05 (0.2)	0.01 (0.08)
	landscape	0.03 (0.04)	0.02 (0.03)

[a] Logging variables not considered as modeling covariates but provided here for reference.

APPENDIX B. Development and transferability of models with nonlinear relationships.

We explored the potential for nonlinear covariate relationships to improve transferability of habitat suitability models by conducting an alternate analysis that allowed for quadratic and interactive covariate relationships. We focused this alternative analysis on models with only remotely sensed data because we had the most data for evaluating transferability and transferability was especially limited for these models.

To allow nonlinear relationships while avoiding the computational demand necessary to consider tens of thousands of candidate models, we conducted model selection in 2 steps. The first step was designed to screen nonlinear relationships. We compared models representing individual quadratic and two-way interactive relationships with equivalent models with only additive linear relationships, i.e. we compared the model

$$\text{logit}(Y) = \beta_0 + \beta_1 x_1 + \beta_2 x_1^2$$

to the model

$$\text{logit}(Y) = \beta_0 + \beta_1 x_1$$

and

$$\text{logit}(Y) = \beta_0 + \beta_1 x_1 + \beta_2 x_2 + \beta_3 x_1 x_2$$

to

$$\text{logit}(Y) = \beta_0 + \beta_1 x_1 + \beta_2 x_2$$

where Y represents the logit-transformed selection probability, β_0 is an intercept term, and β_{1-3} are coefficients describing linear or nonlinear relationships

APPENDIX B TABLE 10. Maximum likelihood parameter estimates (SE) for selected habitat suitability models for nesting Black-backed Woodpeckers at 3 wildfire locations. Candidate models included nonlinear (quadratic and interactive) covariate relationships. Models selected were those with the lowest AIC_c value from each model set. All candidate models from which these models were selected only included remotely sensed covariates. All covariates were scaled to set mean = 0 and SD = 1 (with mean and SD calculated across locations) prior to fitting these models (unlike for models described in main study). Only parameters appearing in at least one selected model are represented.

Parameter	Star Gulch	Toolbox	Tripod
Intercept	−0.03 (0.84)	0.1 (0.15)	1.3 (0.54)
Slope	–	−0.34 (0.14)[a]	–
Burn severity (ΔNBR)	0.71 (0.28)[a]	0.51 (0.11)[a]	1.04 (0.33)[a]
Burn severity $(\Delta\text{NBR})^2$	–	0.07 (0.12)	−0.63 (0.3)[a]
Canopy cover:			
Landscape moderate	−1.38 (1.38)	−0.33 (0.11)[a]	–
Landscape moderate^2	−0.77 (0.52)	0.22 (0.07)[a]	–
Landscape moderate × Slope	–	−0.5 (0.17)[a]	–

[a] Covariate slope parameter estimates whose 95% CIs do not overlap zero.

APPENDIX B TABLE 11. Maximum likelihood parameter estimates (SE) for selected habitat suitability models for nesting Lewis's Woodpeckers at 2 wildfire locations. Candidate models included nonlinear (quadratic and interactive) covariate relationships. Models selected were those with the lowest AIC_c value from each model set. All candidate models from which these models were selected only included remotely sensed covariates. All covariates were scaled to set mean = 0 and SD = 1 (with mean and SD calculated across locations) prior to fitting these models (unlike for models described in main study). Only parameters appearing in at least one selected model are represented.

Parameter	Star Gulch	Toolbox
Intercept	1.18 (0.53)	−0.33 (0.29)
Slope	–	−0.04 (0.4)
Sine aspect	1.23 (0.57)[a]	–
Burn severity (ΔNBR)	1.67 (0.53)[a]	0.78 (0.32)[a]
Sine aspect × ΔNBR	−0.74 (0.48)	–
Canopy cover:		
Landscape moderate	1.16 (0.44)[a]	−0.9 (0.27)[a]
Landscape high	–	0.61 (0.37)
Landscape moderate × Sine aspect	0.8 (0.45)	–
Landscape high × Slope	–	−1.44 (0.5)[a]

[a] Covariate slope parameter estimates whose 95% CIs do not overlap zero.

APPENDIX B TABLE 12. Area under receiver operating curves (AUC) for habitat suitability models measuring discrimination of nest versus non-nest sites for Black-backed and Lewis's woodpeckers ((BBWO and LEWO, respectively). Models were developed and applied at 3 wildfire locations: Star Gulch in Idaho (SG), Toolbox in Oregon (TB), and Tripod in Washington (TP). Models were selected from candidate model sets that only included additive linear covariate relationships (see also Figures 2–4) or from sets that also included nonlinear (quadratic and interactive) relationships.

Species	Development location	Model type	AUC at development location	AUCs at application locations
BBWO	SG	linear	0.715	TP: 0.861, TB: 0.552
		nonlinear	0.74	TP: 0.666, TB: 0.518
	TB	linear	0.66	SG: 0.559, TP: 0.782
		nonlinear	0.693	SG: 0.479, TP: 0.662
	TP	linear	0.863	SG: 0.706, TB: 0.565
		nonlinear	0.828	SG: 0.598, TB: 0.629
LEWO	SG	linear	0.816	TB: 0.43
		nonlinear	0.856	TB: 0.516
	TB	linear	0.728	SG: 0.573
		nonlinear	0.835	SG: 0.527

with covariates $x_{1,2}$. Quadratic and interactive models that showed improved fit (i.e. smaller AIC_c values) than corresponding models with only additive linear effects were retained for consideration. In the second step, we considered all possible combinations of additive linear effects along with those nonlinear effects retained following the initial screening step. We used the same model selection procedure and criteria as implemented for additive linear models that drew our primary focus in this study. We considered all possible quadratic and interactive relationships except for the 3 involving only sine and cosine aspect due to the inherent nonlinearity of aspect (i.e. $sinasp^2$, $cosasp^2$, and sinasp $\times$ cosasp effects were excluded).

All top-ranked remotely sensed models for nesting Black-backed and Lewis's woodpeckers included nonlinear effects (Appendix B Tables 10 and 11). Transferability across wildfire locations did not improve with inclusion of nonlinear effects, and AUC scores at application locations for models with nonlinear effects were often lower than corresponding models with only linear effects (Appendix Table 12). Additionally, many of the nonlinear relationships appearing in selected models (Appendix B Tables 10 and 11) were not as clearly consistent with study species ecology as described in the available literature (see Discussion and references therein). Thus, we considered our focus on additive linear models for this study reasonable and justified.

APPENDIX B TABLE 13. Model selection results for Black-backed Woodpecker nest site selection using remotely sensed covariates at 3 wildfire locations. Ellipses indicate unreported models with $\Delta AIC_c \geq 2$.

Site	Model	$-LL$	K	ΔAIC_c
Star Gulch	ΔNBR + LndCCmd	44.0	3	0.00[a]
	ΔNBR + LndCCmd + LndCChi	43.2	4	0.74
	cosasp + ΔNBR + LndCCmd	43.3	4	0.88
	ΔNBR + LocCCmd + LndCCmd	43.6	4	1.44
	ΔNBR + LndCChi	44.8	3	1.55
	ΔNBR	45.8	2	1.57
	cosasp + ΔNBR + LndCCmd + LndCChi	42.6	5	1.71
	slp + ΔNBR + LndCCmd	43.7	4	1.74
	ΔNBR + LocCCmd	44.9	3	1.89
	. . .			
	Intercept only	49.9	1	7.60
Toolbox	slp + sinasp + ΔNBR	324.4	4	0.00[a]
	slp + sinasp + ΔNBR + LocCCmd	324.0	5	1.29
	slp + sinasp + ΔNBR + LndCCmd	324.2	5	1.67
	slp + sinasp + cosasp + ΔNBR	324.3	5	1.84
	. . .			
	Intercept only	345.2	1	35.54
Tripod	ΔNBR + LndCCmd	23.7	3	0.00[a]
	ΔNBR	25.4	2	1.15
	sinasp + ΔNBR + LndCCmd	23.6	4	1.92
	slp + ΔNBR + LndCCmd	23.6	4	1.94
	cosasp + ΔNBR + LndCCmd	23.6	4	1.98
	. . .			
	Intercept only	36.0	1	20.37

[a] Min AIC_c = 121.1, 1269.1, and 101.5 for Star Gulch, Toolbox, and Tripod locations, respectively.

APPENDIX C. Abridged model selection results reporting negative log-likelihoods (–*LL*), number of parameters (*K*), and AIC_c values for models within 2 AIC_c units of the top-ranked model and an intercept-only model for each of 8 model sets describing habitat suitability for nesting wildfire-associated woodpeckers at 3 wildfire locations.

APPENDIX C TABLE 14. Model selection results for Lewis's Woodpecker nest site selection using only remotely sensed covariates at 2 wildfire locations. Ellipses indicate unreported models with $\Delta AIC_c \geq 2$.

Location	Model	−*LL*	*K*	ΔAIC_c
Star Gulch	sinasp + ΔNBR + LndCCmd	53.0	4	0.00[a]
	sinasp + ΔNBR + LocCCmd + LndCCmd	52.2	5	0.65
	sinasp + ΔNBR + LocCCmd + LndCChi	52.6	5	1.50
	sinasp + cosasp + ΔNBR + LndCCmd	52.6	5	1.57
	sinasp + ΔNBR + LocCCmd + LndCCmd + LndCChi	51.6	6	1.69
	ΔNBR + LndCCmd + LndCChi	53.9	4	1.88
	. . .			
	Intercept only	69.3	1	26.30
Toolbox	ΔNBR + LndCCmd	56.8	3	0.00[a]
	cosasp + ΔNBR + LndCCmd	56.1	4	0.75
	ΔNBR + LocCCmd + LndCCmd	56.4	4	1.28
	slp + ΔNBR + LndCCmd	56.7	4	1.92
	sinasp + ΔNBR + LndCCmd	56.7	4	1.97
	. . .			
	Intercept only	65.2	1	12.73

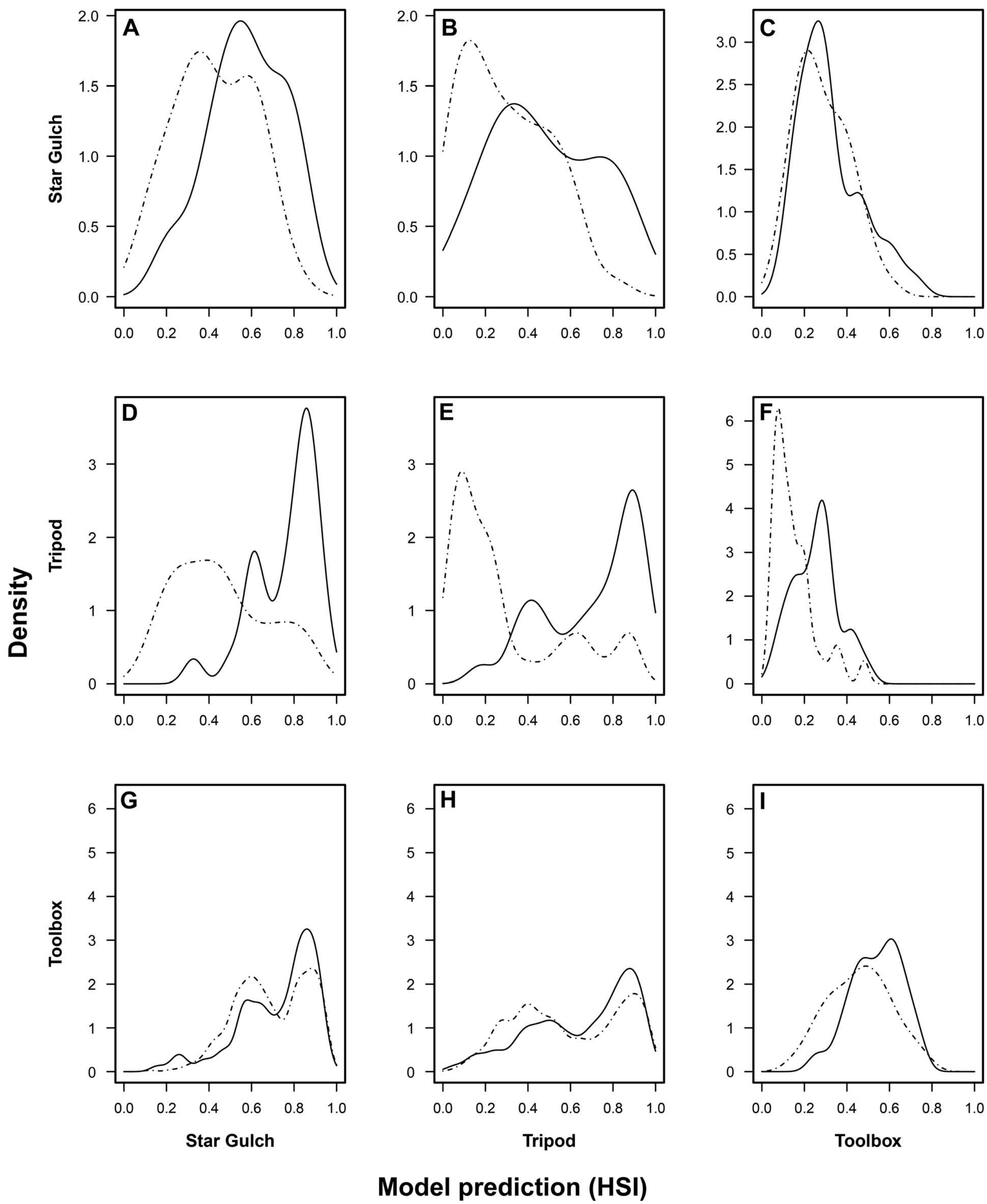
[a] Min $AIC_c = 108.0$ and 1196.8 for Star Gulch and Toolbox locations, respectively.

APPENDIX C TABLE 15. Model selection results for woodpecker nest site selection using both remotely sensed and field-collected covariates at 2 wildfire locations. Models describe nest site selection for Black-backed Woodpecker (BBWO) and Lewis's Woodpecker (LEWO). Ellipses indicate unreported models with $\Delta AIC_c \geq 2$.

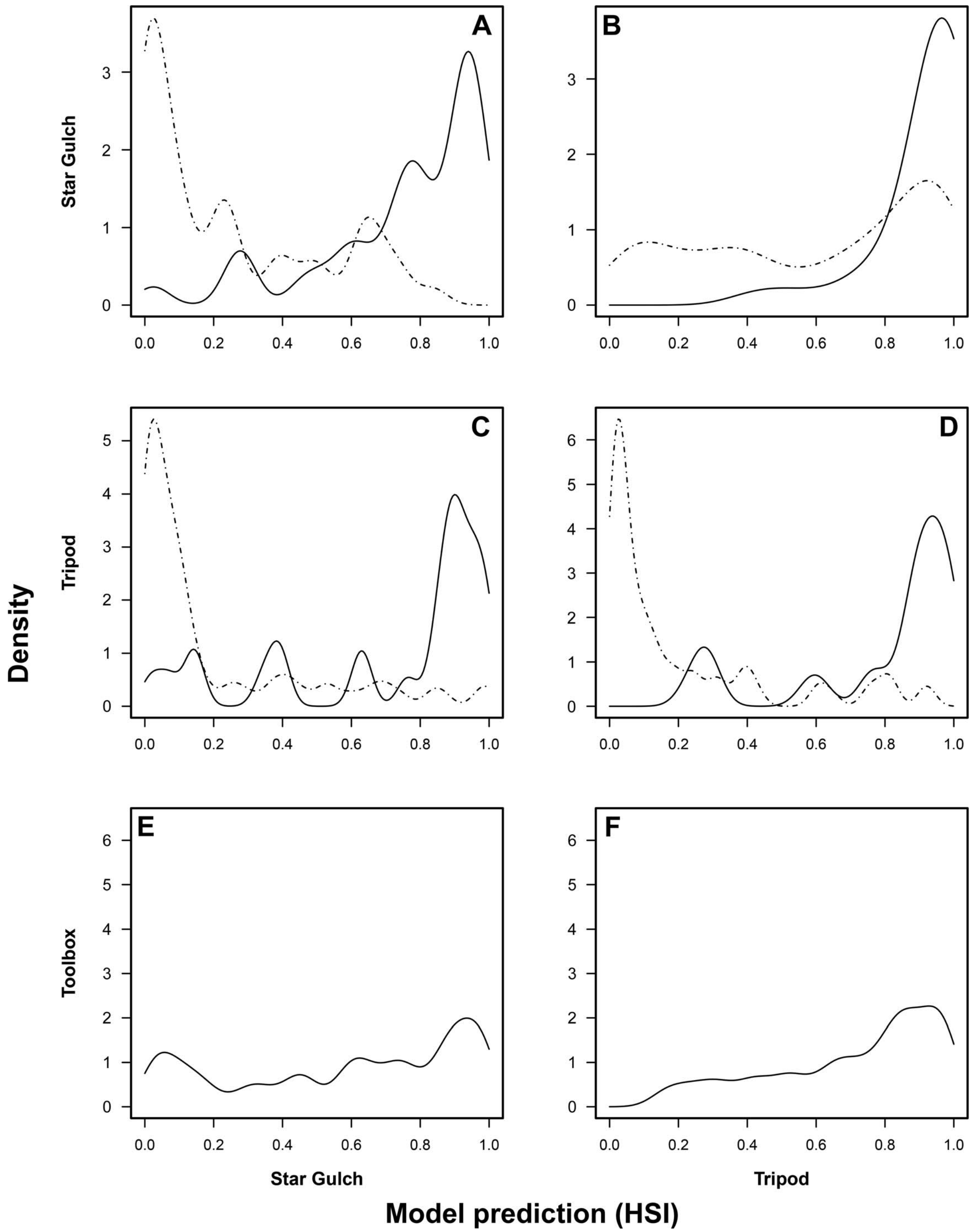
Species	Location	Model	−*LL*	*K*	ΔAIC_c
BBWO	Star Gulch	dbh + snag + cosasp + LndCCmd	27.7	5	0.00[a]
		. . .			
		Intercept only	49.9	1	35.69
	Tripod	dbh + snag + ΔNBR	16.9	4	0.00[a]
		dbh + cosasp + ΔNBR	17.2	4	0.48
		dbh + ΔNBR	18.8	3	1.45
		dbh + ΔNBR + LndCCmd	17.9	4	1.96
		. . .			
		Intercept only	36.0	1	31.81
LEWO	Star Gulch	dbh + snag + cosasp + ΔNBR + LndCCmd	27.1	6	0.00[a]
		dbh + snag + cosasp + LocCCmd + LndCCmd	27.6	6	1.01
		dbh + snag + cosasp + LndCCmd	29.3	5	1.99
		. . .			
		Intercept only	69.3	1	73.48

[a] Min $AIC_c = 83.1$, 79.8, and 63.9 for Black-backed Woodpecker at Star Gulch and Tripod locations, and Lewis's Woodpecker at Star Gulch, respectively.

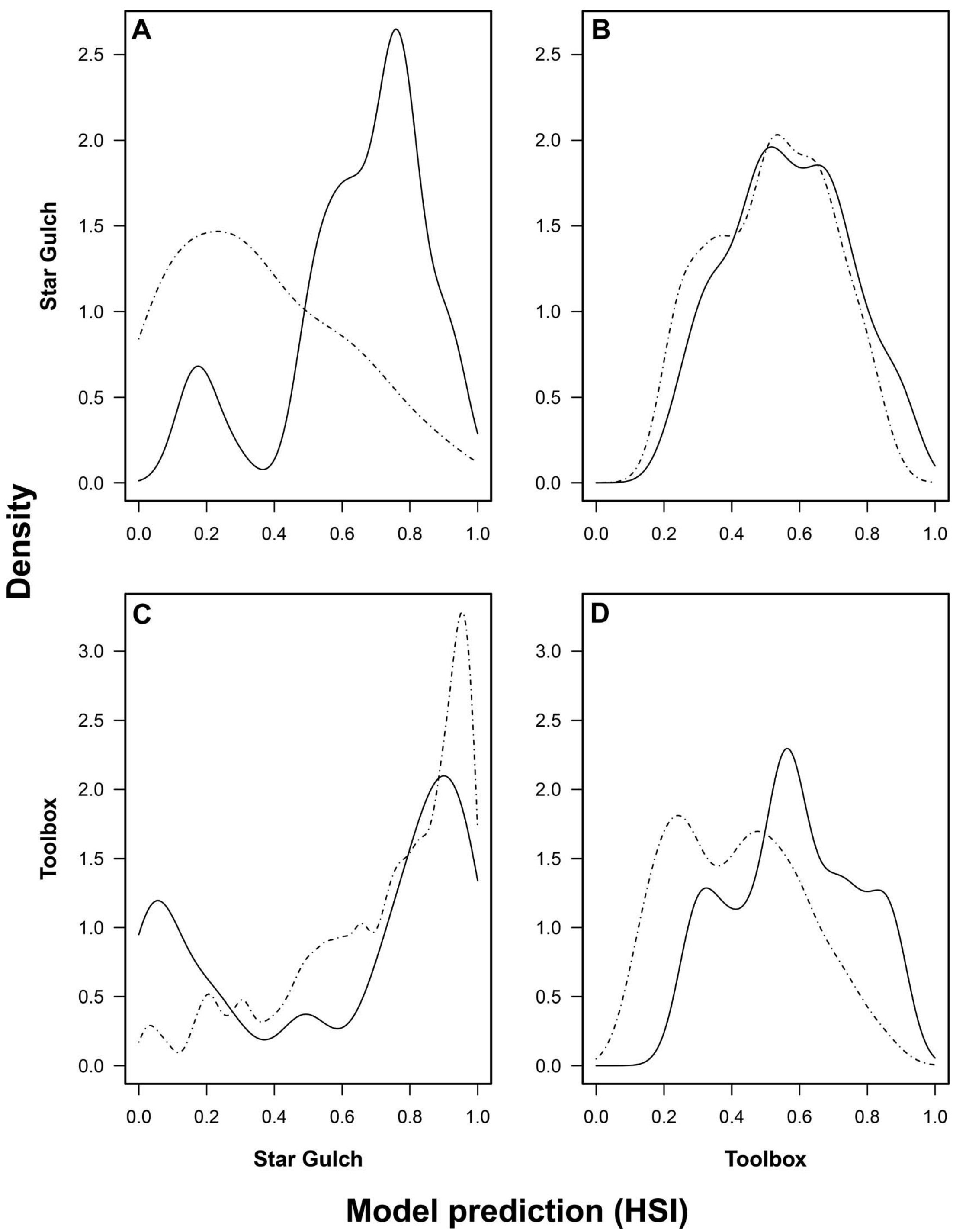
APPENDIX D. Density plots showing smoothed histograms of HSI values for nest (solid lines) and non-nest sites (dotted lines) at locations where habitat suitability models were developed and applied. Plotted values were generated using the "density" function in R (R Core Team 2016) with bandwidth determined by the data (width.SJ function; Sheather and Jones 1991).



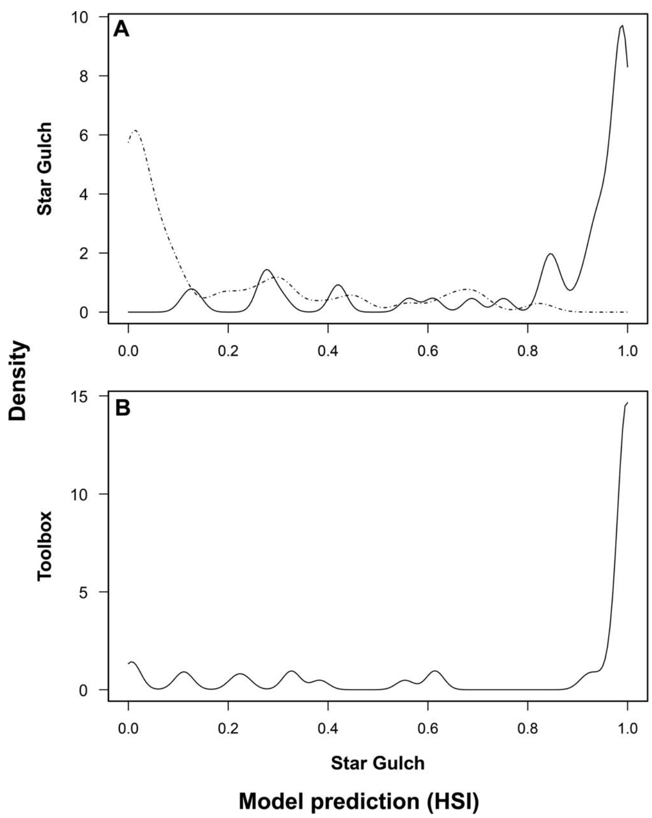
APPENDIX D FIGURE 6. Black-backed Woodpecker density plots for remotely sensed models. Predictions are for wildfire locations where models were developed (**A**, **E**, **I**) and where they were applied to assess transferability (**B**, **C**, **D**, **F**, **G**, **H**).



APPENDIX D FIGURE 7. Black-backed Woodpecker density plots for combination models. Predictions are for wildfire locations where models were developed (**A**, **D**) and where they were applied to assess transferability (**B**, **C, E, F**). Data were only available from nest sites at the Toolbox location (**E, F**).



APPENDIX D FIGURE 8. Lewis's Woodpecker density plots for remotely sensed models. Predictions are for wildfire locations where models were developed (**A**, **D**) and where they were applied to assess transferability (**B**, **C**).



APPENDIX D FIGURE 9. Lewis's Woodpecker density plot for combination model. Predictions are for the Star Gulch wildfire location (Idaho) where the model was developed (**A**) and nest sites at the Toolbox location to assess potential transferability (**B**).