Modeling the impact of climate change and wildfire on the Dusky Grouse (*Dendragapus obscurus*) in the American Southwest: implications for conservation

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ABSTRACT. Climate change is recognized as a threat to the Dusky Grouse (*Dendragapus obscurus*), in part because of changes in weather that might lead to more frequent and severe wildfire that can cause loss of habitat. Our goal was to better understand the geographic range and habitat suitability for the Dusky Grouse in the American Southwest, and to predict impacts of future climate change and recent wildfire on the Dusky Grouse in this region. We developed a species distribution model (SDM) to describe the species’ geographic range in Arizona and New Mexico using climate, topographic, and landcover variables. We modeled the impact of future climate on Dusky Grouse habitat for the years 2041–2060 and 2081–2100 according to two carbon emission scenarios and modeled the loss of habitat due to recent moderate and severe wildfires. Our SDM indicated that the distribution of the Dusky Grouse was best predicted solely by climate variables and consequently is fragmented, particularly in the southern region of the study area. Under future climate scenarios, high quality habitat was predicted to be almost entirely lost regardless of time frame or climate scenario, with the most rapid loss of habitat in the southern region. However, contemporary (2000–2017) wildfires have already caused substantial loss of habitat in the southern region, particularly in the Mogollon Mountains and adjacent areas of southwestern New Mexico. Our finding that loss of habitat due to wildfires may precede and outpace loss of habitat via climate change, suggests that populations may become imperiled or extirpated more quickly than anticipated according to conventional climate models, and that these impacts are likely to first affect trailing-edge populations at the southern extent of the species geographic range, but will spread to more northern regions.

INTRODUCTION

Understanding the factors that determine a species’ geographic range is a fundamental goal of ecology, yet this knowledge is lacking for many populations. At the geographic scale, climate plays a dominant role in shaping species’ ranges because of its influence on physiological tolerances and control on ecological communities (Waite and Strickland 2006, Levin 2012). As a result,
future climatic changes are expected to alter the ranges of many taxa in the coming decades (McDonald et al. 2012, Auer and King 2014, Merker and Chandler 2020). These impacts may be especially strong in trailing-edge populations, despite the propensity for these populations to contain greater genetic diversity than those within contemporary core areas (Hampe and Petit 2005, Ferrari et al. 2018, Merker and Chandler 2020). However, information on the basic biology and status of many of these populations is greatly lacking despite their importance to the overall metapopulation structure (Angert et al. 2011, Cahill et al. 2014). Additionally, because of their isolated nature these populations are often at a greater risk of localized extinction (Cahill et al. 2014) and may require immediate conservation activities in coming years.

The Dusky Grouse (Dendragapus obscurus) is a cold-adapted species associated with coniferous forests with a range that extends from Alaska southward through the Rocky Mountains to Arizona and New Mexico (Zwickel and Bendell 2004). With a lower thermal limit (-5 to -20 °C) than the Rock Ptarmigan (Lagopus muta; Pekins et al. 1992) and a distinct winter diet of conifer needles, the Dusky Grouse represents a unique example of a boreal-adapted species that occurs at low southern latitudes. Genetic data confirmed that the Dusky Grouse is distinct from the Sooty Grouse (D. fuliginosus), which occurs along the Pacific coast from Alaska through the Sierra Nevada to southern California; together these forms were formerly regarded as “Blue Grouse” (Brooks 1929, Barrowclough et al. 2004, Banks et al. 2006). The Dusky Grouse consists of four subspecies, of which D. o. obscurus is the southernmost. Dendragapus o. obscurus occurs in the Wasatch and Uinta mountains (extreme southeastern Idaho, Utah, and extreme southwestern Wyoming), the Southern Rocky Mountains (southeastern Wyoming, Colorado, and north-central New Mexico), and isolated mountain ranges of the American Southwest in Arizona and New Mexico (Zwickel and Bendell 2004, Clements et al. 2021). However, specimens from northern New Mexico (San Miguel and Rio Arriba counties) were genetically isolated and distinct compared to specimens of D. o. obscurus from northern Colorado (Routt Co.) and the Wasatch Mountains in Utah (Utah Co.; Barrowclough et al. 2004). Barrowclough et al. (2004) suggested that the clade represented by the specimens from north-central New Mexico was nearly monophyletic and may represent a distinct species, a hypothesis that may be supported by unique tail plumage within these populations, although they recommended further study before making taxonomic conclusions. No specimens from isolated mountain ranges further south in Arizona or New Mexico were included in the study and hence their phylogenetic relations remain unknown.

Coniferous forests have a relatively expansive and continuous distribution throughout the Southern Rocky Mountains. However, south and west of this region in Arizona and New Mexico, coniferous forests occur as Pleistocene relics stranded on isolated or semi-isolated mountain ranges where high elevations have retained relatively cool, mesic climate (Lomolino et al. 1989). Given limited dispersal ability, populations of Dusky Grouse in this region likely also exist as Pleistocene relics on mountaintop islands of habitat large enough, or interconnected enough, to support persisting populations (Waltari et al. 2007). However, the current distribution and status of Dusky Grouse on these isolated mountaintop forest islands is poorly known, especially in New Mexico where there have been no published studies focused on this species. In Arizona, studies on Dusky Grouse have addressed seasonal food and habitat use (LeCount 1970, Severson 1986) and have suggested a positive relationship between precipitation and population size (Brown and Smith 1980). Further, the general lack of information regarding Dusky Grouse within this region is despite its status as a protected game species. Currently, both Arizona and New Mexico manage annual fall hunting seasons with harvest limits of three grouse per day (New Mexico Department of Game and Fish 2021, Arizona Game and Fish Department 2022). Recent management efforts to translocate Dusky Grouse to establish new populations have often failed, with no explanation as to the cause (Zwickel and Bendell 2004).

Self-sustaining populations of grouse require large areas of interconnected habitat (Storch 2007). Relict populations of Dusky Grouse in the American Southwest are likely facing serious and ongoing conservation issues and the small, isolated nature of their populations likely exacerbate these concerns. By 1928 the Dusky Grouse was considered greatly reduced in numbers in New Mexico and was considered extirpated from Mount Taylor, the Zuni Mountains, and the Black Range (Ligon 1927, Bailey 1928). By the 1960s populations of the Dusky Grouse in New Mexico outside the north-central mountains were thought to persist in only four mountain ranges in the southwestern part of the state (Mogollon, Tularosa, San Francisco, and San Mateo; Ligon 1961). Furthermore, Merrill (1967) concluded that they could disappear entirely from this region. Even in their core range at high elevations in the Mogollon Mountains they were considered uncommon (Hubbard 1965). Reasons provided for the apparent decline included hunting, logging, drought, and especially overgrazing by livestock (Bailey 1911, Ligon 1927, Merrill 1967). Dusky Grouse require grass and forb ground cover during the breeding season to conceal nests and thus excessive livestock grazing was blamed for the near lack of recruitment during some years, as well as their overall scarcity (Ligon 1927, Bailey 1928). Those observations led to a call to protect Dusky Grouse and to end poor grazing management in New Mexico (Bailey 1928). Subsequent research has confirmed that grazing and drought can result in lowered abundance of Dusky Grouse through reduced herbaceous vegetation (Mussel 1963).

More recently, the Dusky Grouse was recognized as a “climate threatened” species by the National Audubon Society (National Audubon Society 2013, 2015, Wilsey et al. 2019a). Climate models predicted substantial reductions in areas of suitable “climate refuge” for the Dusky Grouse relative to current conditions (National Audubon Society 2013, Wilsey et al. 2019a). In part, this vulnerability might be explained by the species’ dependence on high elevation coniferous forests during the winter because these forests are highly susceptible to degradation and loss due to future climatic change (Thorne et al. 2018, Maxwell and Scheller 2020). Further, decreasing annual precipitation, decreased snowmelt, and increasing temperatures associated with climate change are expected to facilitate larger and more severe wildfires in the American Southwest in the coming century (Overpeck et al. 2013). Already, the largest wildfires on record in Arizona and New Mexico recently occurred in the only two mountain ranges in the southern part of the region where Dusky Grouse are known.
to persist, including the 2011 Wallow Fire in the White Mountains, Arizona, which burned 2178 km² (Kennedy and Johnson 2014) and the 2012 Whitewater-Baldy Complex Fire in the Mogollon Mountains, New Mexico, which burned 1204 km² (Burned Area Emergency Response 2012). These wildfire events could further reduce or fragment already small grouse populations in the region and are a major cause of conservation concern.

Understanding the environmental drivers that define a species’ geographic range is an essential goal of management and conservation, particularly for trailing edge populations along southern range limits that may be particularly susceptible to future changes. Species distribution models (SDMs) use species’ occurrence records along with environmental variables to produce models of the species’ distribution that can also be interpreted as habitat suitability (Guisan and Zimmermann 2000, Guisan et al. 2017). SDMs have been used to identify environmental variables that influence species’ distribution, predict the effects of climate change on species’ ranges, pinpoint areas of core habitat for endangered species, and predict new areas where a species may occur (Guisan and Zimmermann 2000, Guisan et al. 2013, Goljani Amirkhiz et al. 2018). The objectives of our study were to (1) create a SDM that predicts the distribution and habitat suitability of the Dusky Grouse at the southern extent of the species’ geographic range, (2) identify environmental variables that limit the geographic range of the Dusky Grouse, (3) predict future habitat for Dusky Grouse under climate change scenarios, (4) predict loss of winter habitat for Dusky Grouse due to recent wildfires, and (5) recommend strategies for the effective conservation and management of this species in the region.

METHODS

Overview of modeling approach

Habitat selection occurs at multiple scales (Johnson 1980), and consequently it is important to correctly match methods and sources of data to the scale of investigation. Our goal was to create a SDM that predicts the geographic range of the Dusky Grouse in the American Southwest, which is equivalent to first order selection sensu Johnson (1980). To accomplish this, we used spatial environmental data in a geographic information system (GIS), which we analyzed using Maxent version 3.4.1.k (Phillips et al. 2006, 2017). Maxent is a program that uses a machine learning algorithm to model the distribution of a species based on occurrence locations and spatial data layers. Maxent does not require absence points, which was useful for our study because no formal presence-absence survey data exist for Dusky Grouse in our study area. In addition, it allowed us to use museum records and observational data as sources of data for modeling (Elith et al. 2011). Maxent is commonly used to construct SDMs in part because it performs better than other presence-only methods, especially when sample sizes are small (Elith et al. 2006, 2011). However, Maxent is prone to overfitting and only performs well if its assumptions are met and its settings are tuned (Merow et al. 2013, Morales et al. 2017). Consequently, our methods were based on the recommendations of Merow et al. (2013) and were designed to reduce potential sources of introduced bias in our SDM. Model outputs are a relative likelihood of occurrence of the species, which can be interpreted as habitat suitability (Guillera-Arroita et al. 2015).

Study area

The study area was the states of Arizona and New Mexico, which represent the southernmost range limits of the Dusky Grouse. This region has diverse topography, ranging in elevation from 21 m to 4013 m, which results in different vegetation communities occurring along elevational gradients (Brown 1994). Within the study area, Dusky Grouse are primarily associated with subalpine coniferous forest and upper mixed coniferous forest. Subalpine coniferous forest is dominated by Engelmann spruce (Picea engelmannii) and subalpine fir (Abies lasiocarpa) and it is the highest elevation forest type, generally occurring above 2500 m to treeline (~3300 m; Brown 1994). The cold, mesic upper mixed coniferous forest is dominated by Douglas-fir (Pseudotsuga menziesii), white fir (Abies concolor), blue spruce (Picea pungens), and quaking aspen (Populus tremuloides; Brown 1994). These coniferous forests, particularly the subalpine coniferous forest, which only occur on the highest peaks, are considered essential winter habitat for Dusky Grouse (Ligon 1927, Brown 1989). Further, montane and subalpine meadows that occur in openings within these forests are important for nesting and foraging during the breeding season (Zwickel and Bendell 2004). Vegetation types at elevations below the upper mixed coniferous forest zone—which become progressively warmer and more arid—include coniferous woodlands, grasslands, and deserts, which likely limit the potential for occurrence or dispersal by Dusky Grouse (Zwickel and Bendell 2018).

Occurrence records

We compiled occurrence records of Dusky Grouse within the study area from museums, observational databases, credible observations made by knowledgeable professionals, and the literature. We searched for museum specimen records using Vertnet (http://www.vertnet.org) and Arcoto (https://arctos.database.museum). We also searched for specimens in the New Mexico State University Vertebrate Museum, National Museum of Natural History, and the University of Arizona Museum of Natural History. We searched for observation records in the New Mexico Ornithological Society Observation Database (http://www.nmbirds.org), Arizona Field Ornithologists Sightings Database (http://www.azfo.org), eBird (Sullivan et al. 2009; https://www.ebird.org), and iNaturalist (https://www.inaturalist.org). We georeferenced occurrence records lacking global positioning system coordinates using DeLorme Topo USA Version 5.0 (DeLorme 2004, Yarmouth, Maine, USA). We followed Frey et al. (2013) to assign each record to six precision classes (H: < 30 m, I: 30–500 m, J: 500–1000 m, K: 1000–2000 m, L: 2000–3000 m, and M: > 3000 m) that represented the likely deviation of the coordinate relative to the actual location and to four reliability classes (A: museum specimen or photo evidence, B: expert observation, C: non-expert observation, and X: erroneous record). We excluded records in precision class L, M, and N, reliability class X, and translocations outside the historical range. We excluded records in reliability class C that were below 2316 m elevation north of latitude 35°N and below 2499 m elevation south of latitude 35°N, which we considered not suitable and therefore likely misidentifications. Additionally, we removed records that were outside the temporal range of our environmental predictor layers. Finally, we mapped the remaining occurrence records using ArcGIS version 10.8 software (Environmental Systems Research Institute 2011, Redlands, California, USA) and used them to create the SDM.
Environmental predictors

We developed hypotheses about environmental factors that might structure the distribution of the Dusky Grouse in our study area and selected bioclimatic and biophysical environmental layers to represent those hypotheses for testing (see Appendix 1 for the hypotheses, rationales, and variable definitions). We did not consider environmental variables that were highly correlated ($r > 0.9$) to reduce redundancy. The bioclimatic variables were obtained from WorldClim Version 2.1 (https://www.worldclim.org) representing years 1970–2000 and depicting measures of annual trends, seasonality, and limiting factors (Hijmans et al. 2005, Fick and Hijmans 2017). We obtained landcover data from the Southwest Regional GAP Analysis (https://www.swregap.org), but combined some landcover types that were similar (e.g., Rocky Mountain subalpine mesic meadow and Southern Rocky Mountain montane-subalpine grassland) to reduce the number of classes (see Appendix 2 for the reclassified landcover types). We included topographical variables (heat load index and terrain ruggedness index) because of their possible influence on local environment and vegetative conditions. We did not include elevation because it directly influences climate and we aimed to model climate variables directly without this influence. We generated heat load index using the ArcGIS Geomorphology and Gradient Metrics toolbox version 2.0 (Evans et al. 2014) to calculate the relationship between slope and aspect ratios following the methods of McCune and Keon (2002). We generated terrain ruggedness index, a measure of landscape heterogeneity, in ArcGIS Version 10.8 by subtracting the elevation layer from nearby grid cells following the methods of Riley et al. (1999). We included annual normalized difference vegetation index (NDVI) because it indicates plant “greenness” or productivity and canopy cover, and models including this variable can outperform those without it (Amaral et al. 2007). For NDVI we averaged one year of 14-day survey window data from the Moderate Resolution Imaging Spectroradiometer database (https://modis.gsfc.nasa.gov/) for 2017 to represent annual conditions across the study area. Environmental data layers were generated at a 1-km² spatial resolution.

Species distribution model

Prior to model construction, we restricted our occurrences to the temporal window of our environmental predictor layers (1970–2017). Next, to reduce the effect of sampling bias and spatial autocorrelation, we rarefied occurrence records to 1 km. These steps allowed us to pair the occurrences with the temporal and spatial resolution of our environmental predictor layers. Maxent compares environmental conditions at the occurrence locations with those at random background locations to predict the species’ relative likelihood of occurrence (Phillips et al. 2006, Merow et al. 2013). We restricted the background extent to only areas where Dusky Grouse could occur by creating a buffer around each occurrence point using the maximum dispersal distance of the species (35 km; Barrowclough et al. 2004).

Maxent is capable of making overly complex models, which may be less interpretable, more sensitive to sampling bias, and prone to falsely inflated model evaluation metrics (Merow et al. 2013). Thus, to prevent these issues we controlled model complexity by reducing multicollinearity, selecting the best subset of covariates, and tuning the regularization parameter ($\beta$ multiplier), which is a penalty coefficient to reduce overfitting (Anderson and Gonzalez 2011, Warren et al. 2014). We accomplished this via a series of steps following the methods of Warren et al. (2014). We began the modeling process with an initial candidate pool of 14 variables (4 biophysical, 10 climate) that we hypothesized may be important in determining the geographic range of the species within the study area (Appendix 1). First, we generated a set of models using the full variable suite where we manipulated the $\beta$ multiplier from 0 to 15 at an increment of 0.1 (Warren et al. 2014). Next, we used ENMTools (Warren et al. 2010) to select the best supported model based on the lowest AIC$_C$ value (Akaike’s 1974 information criteria corrected for small sample size; Burnham and Anderson 2002). From this starting model, we removed all variables with < 5% contribution and designated the highest contributing variable as the most important variable. If the next highest contributing variable was correlated at $|r| > 0.7$ with the most important variable, it was discarded. If it was not correlated, this variable was retained along with the remaining variables that contributed over 5% to this preliminary model. We then re-ran the model, continually retaining the most important variable and removing correlated variables ($|r| > 0.7$) or variables with < 5% contribution. We continued this process until all variables were uncorrelated and contributed greater than 5%; this suite of variables became the final variable set. Although these methods were designed in part to reduce collinearity, recent research suggests that Maxent is robust against these effects (Feng et al. 2019). Finally, we validated our models by calculating the AUC value for the top model at each step of the variable selection process, following the recommendations of Vignali et al. (2020), to document how the reduction of variables improved the predictive power of each subsequent model within this framework.

After developing the final variable set, we re-tuned the model by generating models where we adjusted the $\beta$ multiplier from 0 to 15 at increments of 0.1 and used ENMTools to select the model with the lowest AIC$_C$ value. Using this final suite of variables and the adjusted $\beta$ multiplier, we ran the final model with the default settings for convergence threshold, maximum iterations, and 20 bootstrap model replicates. The bootstrap replicated run type was selected because of the small number of occurrence locations (Wu et al. 2009). To maintain a larger sample size, test data were not separated from training data. Maxent models assume that species are at equilibrium with the environmental predictor layers used to fit the model and consequently extrapolation outside the range of variation of the environmental layers can lead to misinterpretation of model results (Pearson et al. 2006, Buisson et al. 2010). Thus, the environmental predictor layers for our model were generated in the raster format in order to perform a multivariate environmental similarity surface (MESS) analysis, as suggested by Elith et al. (2010), by using the MESS analysis setting in Maxent. The MESS analysis allowed us to compare the similarity of environmental predictors at the occurrence locations and the projection dataset, which was used to identify areas where conditions were outside of the range of the training data. Model predictions outside of this range may be unreliable.

It has been recommended that multiple evaluation metrics be used for evaluating Maxent models (Fourcade et al. 2018). Therefore, we evaluated our model using the area under the receiving
operator characteristic curve (AUC), sensitivity, specificity, and true skill statistic (TSS; Landis and Kock 1977). The use of AUC is important for evaluating the model’s ability to determine which records were likely accurate (1.0), compared to those records that represented false occurrences or models with limited predictive power (0.5; Tingley and Herman 2009). We calculated AUC values using a block-partitioned k-fold cross-validation using the package “ENMeval” (Muscarella et al. 2014) in Program R (R Core Team 2018), withholding 75% of the occurrence records for training and using the remaining 25% for testing. The block-partitioned method partitions occurrence records by latitude and longitude into k bins of approximately equal size; and we defined k = 4 to determine our training and testing samples. This method is recommended for situations where models are transferred across time, particularly under scenarios where non-analog conditions may occur (Muscarella et al. 2014). The TSS represents matches and mismatches between occurrences and model predictions and ranges from -1 to +1, where +1 indicates perfect model agreement and values < 0 represent random predictions (Fielding and Bell 1997). We used TSS to define model performance as: poor (0–0.3), moderate (0.31–0.6), and substantial (> 0.6; Allouche et al. 2006). We evaluated the variable response curves to understand the relationship between the relative likelihood of occurrence and individual environmental predictors. We displayed our model as a map in logistic output format, which describes the relative likelihood of occurrence of the species (i.e., which can be interpreted as habitat suitability) as a continuous variable from a range of 0 (no likelihood of occurrence) to 1 (occurrence extremely likely), which we interpreted as habitat suitability (Phillips and Dudik 2008). We compared the map created from the model with occurrence records of Dusky Grouse to confirm if the model accurately portrayed the species distribution. For interpretation, we also created a map that displays five habitat suitability classes based on the relative likelihood of occurrence: 0–0.2 no/very low suitability; 0.21–0.4 low suitability; 0.41–0.6 moderate suitability; 0.61–0.8 high suitability; 0.81–1.0 very high suitability.

**Future climate predictions**

To predict the geographic range of an organism in future climates, it requires a SDM based on current climate variables, which represents the predicted “climate envelope” of the species within the study area (Thomas et al. 2004, Ibáñez et al. 2006). The climate envelope model (CEM) describes the species’ niche and consequently the relationships are assumed to remain constant through time as they are based on the species’ biology and evolutionary history (Pearson and Dawson 2003, Fitzpatrick et al. 2008). To predict the species’ geographic range at a future time, the CEM is projected onto data layers that represent the climate in the future time (Araújo and Peterson 2012, Watling et al. 2013a, b).

We were unable to use our SDM for the climate predictions because it was created with 1-km spatial resolution data, while the future climate data were available at 4.5-km spatial resolution (https://www.worldclim.org). Therefore, we created a new model to serve as the CEM based on an initial candidate pool of 12 climate variables that we hypothesized may be important to the species distribution in the study area; the 12 variables represented current climate (1970–2000) at 4.5-km spatial resolution (Appendix 1). We followed the same procedures for constructing, evaluating, and interpreting the CEM as we did for the SDM. Changes in coarseness of climate layers can produce different model results (Franklin et al. 2013). Consequently, to ensure that the SDM and the CEM made similar predictions despite a difference in resolution, we measured the degree of similarity between the habitat suitability values of both models using the niche overlap feature in ENMTools. This analysis measures model overlap using Schoener’s D (Schoener 1968), J statistic (Warren et al. 2008), and relative rank (Warren and Seifert 2011), where each value ranges from 0 (no agreement) to 1 (full agreement). The D and J statistics standardize output cells from the models so that they sum to 1 across the model extent and the difference between relative likelihood of occurrence cell values from competing models are compared. The relative rank estimates the probability that the relative likelihood of occurrence for a grouping of cells is similar for competing models, rather than at individual cells (Warren et al. 2010, Warren and Seifert 2011).

To predict how the geographic range of the Dusky Grouse might change in the future, we projected the CEM onto data layers representing future climate conditions. For the climate projections we used the Coupled Model Intercomparison Project phase 6 (CNRM-CM6-1) global climate model calibrated for WorldClim data (Eyring et al. 2016, Voldoire et al. 2019). We chose the CNRM-CM6-1 global climate model because it has been shown to not over or under predict future changes in seasonal precipitation or extended dry periods within the American Southwest (Srivastava et al. 2020, Akinsanola et al. 2020a, 2020b).

We projected the CEM onto GIS layers representing climate at two time periods, 2041–2060 and 2081–2100, and based on two climate change scenarios: an optimistic low CO$_2$ emission scenario (Shared Socioeconomic Pathways [SSP 2–4.5]) and a pessimistic high CO$_2$ emission scenario (SSP 5–8.5). The SSP 2–4.5 scenario represents warming of ~3 °C by the year 2100, with an increase in CO$_2$ emissions until 2060 followed by a gradual decrease in emissions through the year 2100 (Riahi et al. 2017). In the SSP 5–8.5 scenario, reliance on fossil fuels continues to drive economic development, resulting in projected warming of ~5 °C by the end of 2100 (Riahi et al. 2017). We performed a MESS analysis for the CEM, which allowed us to compare similar and novel (negative values) environmental conditions across all future climate scenarios.

To understand how the geographic range of the Dusky Grouse is predicted to change under future climate scenarios, we first converted the continuous logistic outputs of the CEM and the future projections into five habitat suitability classes: 0–0.2 no/very low suitability; 0.21–0.4 low suitability; 0.41–0.6 moderate suitability; 0.61–0.8 high suitability; 0.81–1.0 very high suitability.
area, we also were interested in understanding if recent wildfires had caused loss of habitat for the Dusky Grouse at smaller orders of selection, specifically winter roosting and foraging habitat. We considered the mixed coniferous and subalpine coniferous forests to represent winter habitat for Dusky Grouse. To understand how recent wildfires may have affected winter habitat for the Dusky Grouse, we obtained burn severity data from the Monitoring Trends in Burn Severity (MTBS) program (https://www.mtbs.gov) for all fires that occurred in the study area for the years 2000 to 2017. We selected this temporal extent because it captures the most extensive recent fire history and includes “megafires” (Stephens et al. 2014, Mueller et al. 2020), which are an increasing threat across this region. We extracted the Moderate and Severe burn severity categories for each fire that overlapped habitat for the Dusky Grouse as predicted by our SDM. We defined Dusky Grouse habitat as habitat suitability classes 0.4–1.0 in the SDM. We used the Moderate and Severe burn severity categories because these classes reflect widespread mortality and damage to conifer trees in mixed coniferous and subalpine coniferous forests (USDA Forest Service 2010). The Moderate burn severity class indicates that the tree canopy was mostly scorched or consumed, while the Severe burn severity class indicates that the canopy foliage was completely consumed (USDA Forest Service 2010). These conditions would largely or completely eliminate winter roosting and foraging habitat for Dusky Grouse.

To assess the extent of loss of winter habitat for the Dusky Grouse due to wildfire, we calculated the area that the Moderate and Severe burn severity classes overlapped Dusky Grouse predicted habitat and expressed the totals as percent of available habitat. To understand regional differences, we calculated the percent loss for each state, for the northern and southern regions (divided at 35° latitude), and for the Gila National Forest subregion of southwestern New Mexico (i.e., Catron, Grant, and Sierra counties). We excluded areas where the SDM predicted habitat outside of the historical range of the Dusky Grouse (e.g., Pinaleño Mountains, AZ, Mogollon Rim, AZ, Sacramento Mountains complex, NM) to provide a realistic assessment for managers on the impacts of fire on potential grouse habitat.

RESULTS

Species distribution model

We found 783 occurrence records representing 430 unique locations for Dusky Grouse in Arizona and New Mexico (Appendix 3 and 4), of which 137 were used for modeling (Fig. 1). Following the variable selection procedure, the final SDM included five variables: precipitation of warmest quarter, mean diurnal range, annual mean temperature, precipitation of driest month, and mean temperature of wettest quarter (Table 1). The SDM with five variables and based on 137 occurrence records met the rule of thumb of 10 occurrence records per variable, which reduces the risk of overfitting the model (Warren et al. 2014). The SDM used a β multiplier of 2.7 (Table 2) and feature classes: hinge, product, linear, threshold, and quadratic. The SDM had good model performance based on AUC metrics and the TSS indicated substantial support (Table 2). The map depicting the continuous likelihood distribution (0–1) based on the SDM showed overlap of known grouse occurrences (Appendix 4) with areas of high relative likelihood of occurrence (Fig. 2). The model improved at each stage of the validation process, from a starting point of AUC = 0.899 and an ending value of AUC = 0.909 (Appendix 5). The variable with the highest percent contribution to the model was precipitation of warmest quarter (39.2%) and exhibited an optimum range that peaked at ~330 mm (Fig. 3). The next highest contribution was mean diurnal range (19.8%), which was
Fig. 2. Species distribution model for the Dusky Grouse (*Dendragapus obscurus*) in the American Southwest. Relative likelihood of occurrence of the species is represented across a continuous distribution from high likelihood (1.0-red) to no likelihood (0-white). Black lines are state and county borders.

Historical records of grouse were available from several mountain ranges that were not included in our modeling (Appendix 3 and 4), yet those ranges were predicted to have moderate likelihood of occurrence (e.g., Chuska Mountains, Sandia Mountains, Magdalena Mountains, San Mateo Mountains, Black Range). The MESS analysis indicated that the following regions had variables outside the range of the training data and thus may not predict well: Mojave and Sonoran desert regions of extreme western and southwestern Arizona, Lake Powell region in northcentral Arizona, high elevations of south-central Arizona, the Carrizo Mountains in northeastern Arizona, the Chuska Mountains in northeastern Arizona and northwestern New Mexico, and the Sacramento Mountains complex and Guadalupe Mountains in south-central New Mexico (Appendix 6).

Areas predicted to have the highest relative likelihood of occurrence for the Dusky Grouse included the Kaibab Plateau, San Francisco Peaks, White Mountains, and Pinaleño Mountains in Arizona, and the San Juan Mountains, Sangre de Cristo Mountains, Jemez Mountains, Mount Taylor, Mogollon Mountains, and Sacramento Mountains Complex (Capitan, White, and Sacramento mountains) in New Mexico (Fig. 2).

Table 1. Percent contributions for environmental predictors retained in the final species distribution model and climate envelope model for the Dusky Grouse (*Dendragapus obscurus*) in the American Southwest.

<table>
<thead>
<tr>
<th>Environmental Predictor</th>
<th>Percent Contribution</th>
</tr>
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<tbody>
<tr>
<td>Species distribution model</td>
<td></td>
</tr>
<tr>
<td>Precipitation of Warmest Quarter</td>
<td>39.2</td>
</tr>
<tr>
<td>Mean Diurnal Range</td>
<td>19.8</td>
</tr>
<tr>
<td>Annual Mean Temperature</td>
<td>14.0</td>
</tr>
<tr>
<td>Precipitation of Driest Month</td>
<td>13.5</td>
</tr>
<tr>
<td>Mean Temperature of Wettest Quarter</td>
<td>13.4</td>
</tr>
<tr>
<td>Climate envelope model</td>
<td></td>
</tr>
<tr>
<td>Maximum Temperature of Warmest Month</td>
<td>69.4</td>
</tr>
<tr>
<td>Precipitation of Wettest Quarter</td>
<td>22.1</td>
</tr>
<tr>
<td>Isothermality</td>
<td>8.5</td>
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</tbody>
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Table 2. Model regularization multiplier and predictive accuracy statistics for the species distribution model and climate envelope model for the Dusky Grouse (*Dendragapus obscurus*) in the American Southwest.

<table>
<thead>
<tr>
<th>Model</th>
<th>Years</th>
<th>Regularization Multiplier (β)</th>
<th>Training AUC</th>
<th>Sensitivity</th>
<th>Specificity</th>
<th>True Skill Statistic</th>
</tr>
</thead>
<tbody>
<tr>
<td>Species distribution model</td>
<td>1970–2017</td>
<td>2.7</td>
<td>0.909</td>
<td>0.932</td>
<td>0.775</td>
<td>0.707</td>
</tr>
<tr>
<td>Climate envelope model</td>
<td>1970–2000</td>
<td>7.5</td>
<td>0.899</td>
<td>0.893</td>
<td>0.789</td>
<td>0.682</td>
</tr>
</tbody>
</table>

Climate predictions

The CEM had good model performance based on AUC metrics and the TSS, which indicated substantial support (Table 2). The CEM improved at each stage of the validation process, beginning
at AUC = 0.873 and concluding with AUC = 0.899 (Appendix 5). The CEM included three variables: maximum temperature of warmest month (69.4% contribution), precipitation of wettest quarter (22.1% contribution), and isothermality (8.5% contribution). Relative likelihood of occurrence of the Dusky Grouse exhibited a positive association with precipitation of wettest quarter and a negative association with maximum temperature of the warmest month and isothermality (Appendix 7). The spatial patterns of predicted grouse habitat were visually similar between the SDM and CEM (Fig. 2 and Appendix 7) and the two models exhibited high similarity based on all three metrics: D (0.68); I (0.91); and relative rank (0.89).

Based on projections of the CEM onto data layers representing future climate, the geographic range of the Dusky Grouse within the study area is predicted to shrink over time, with the magnitude dependent on the carbon emissions scenario and region (Fig. 4; Table 3). The highest quality habitat (> 0.6) was predicted to be completely lost in both time periods and according to both emission scenario, with exception of a relatively small area remaining under the SSP2-4.5 scenario in the 2041–2060 time period. Areas of moderate habitat suitability were predicted to be mostly lost by the 2041–2060 time period, and completely lost by the 2081–2100 time period under the SSP 5–8.5 emission scenario. The southern region was predicted to experience more rapid loss of habitat than the northern region, with many patches of habitat completely eliminated by the 2041–2060 time period (Fig. 4; Table 3).

**DISCUSSION**

**Role of climate in determining the southern range limits of the Dusky Grouse**

Our SDM suggests that climate is the primary limiting factor structuring the geographic range of the Dusky Grouse at its southern limits in the American Southwest; other variables representing vegetation and topography were not significant in our analysis. This finding supports the hypothesis that climate is the primary driver defining the distribution of trailing-edge populations (Cahill et al. 2014, Lynch et al. 2014, Coristine and Kerr 2015). At warm range boundaries, climate can structure...
distribution directly by limiting physiological processes (Cahill et al. 2014) or indirectly through influences on vegetation (Brovkin 2002). Although there currently is little information about the physiology of Dusky Grouse that relates directly to climate, such as its upper critical temperature threshold or the role of snow (or snow quality) in thermoregulation during winter, our model supported general hypotheses about the potential influence of the climate variables on the species' physiology and required vegetation.

### Table 3. Area of predicted habitat (km²) and cumulative percent lost for the Dusky Grouse (*Dendragapus obscurus*) in the American Southwest under current and future climate scenarios.

<table>
<thead>
<tr>
<th>Habitat Suitability Class</th>
<th>Current</th>
<th>2041–2060</th>
<th>2081–2100</th>
<th>2041–2060</th>
<th>2081–2100</th>
</tr>
</thead>
<tbody>
<tr>
<td>North region</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>0.4–0.6</td>
<td>4168.7</td>
<td>484</td>
<td>88.4</td>
<td>123.1</td>
<td>97.0</td>
</tr>
<tr>
<td>0.6–0.8</td>
<td>1838.2</td>
<td>14.9</td>
<td>99.2</td>
<td>0</td>
<td>100</td>
</tr>
<tr>
<td>0.8–1.0</td>
<td>526.4</td>
<td>0</td>
<td>100</td>
<td>0</td>
<td>100</td>
</tr>
<tr>
<td>Northern subregion</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>0.4–0.6</td>
<td>3442.8</td>
<td>424.5</td>
<td>87.7</td>
<td>87</td>
<td>97.5</td>
</tr>
<tr>
<td>0.6–0.8</td>
<td>1653.5</td>
<td>14.9</td>
<td>99.1</td>
<td>0</td>
<td>100</td>
</tr>
<tr>
<td>0.8–1.0</td>
<td>467.0</td>
<td>0</td>
<td>100</td>
<td>0</td>
<td>100</td>
</tr>
<tr>
<td>Southern subregion</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>0.4–0.6</td>
<td>725.9</td>
<td>59.4</td>
<td>91.8</td>
<td>36.1</td>
<td>95.0</td>
</tr>
<tr>
<td>0.6–0.8</td>
<td>184.7</td>
<td>0</td>
<td>100</td>
<td>0</td>
<td>100</td>
</tr>
<tr>
<td>0.8–1.0</td>
<td>59.4</td>
<td>0</td>
<td>100</td>
<td>0</td>
<td>100</td>
</tr>
</tbody>
</table>

Organisms may select different aspects of the environment at different scales of habitat selection (Johnson 1980). The SDM and CEM were designed to evaluate the broadest (first order) scale of selection-selection of the geographic range. Consequently, the models likely predict more habitat than actually exists because Dusky Grouse also require specific habitat conditions at finer scales of selection. For instance, at finer scales of selection Dusky Grouse rely on Douglas-fir needles and other parts of conifer trees as their winter food, primarily selecting younger needles from the upper canopy of large (mean 49 cm dbh) and old (mean 235 years old) trees (Remington and Hoffman 1996). During winter, Dusky Grouse roost in the largest Douglas-fir or subalpine fir trees that have a structure providing a thermally protected microclimate (Severson 1986, Cade and Hoffman 1990, Pekins et al. 1989). During spring through fall, male Dusky Grouse may continue to use conifer forests, again selecting the largest Douglas-firs for roosts, while females use bunchgrass meadows and other open areas with adequate herbaceous cover for nesting and rearing young (Musselh 1963). These finer scale habitat requirements are nested within the higher order selection of the geographic range; the species cannot persist without both. The climate variables in our models likely have direct or indirect influence on the availability of these finer scale resources. For instance, climate is the major factor that determines the biotic communities selected for the establishment of grouse home ranges (Brown 1994). The conifer trees used by Dusky Grouse require cold winter temperatures to prepare for summer growth (Ford et al. 2016) and to resist bark beetles and other pests (Raffa et al. 2015); thus, winter roost sites and food resources may be limited by warm temperatures. Subalpine and montane meadows require adequate precipitation for lush growth; thus, low precipitation could increase predation rates and decrease nest success (Brown and Smith 1980, Zwickel and Bendell 2004).

### Table 4. Area of current predicted habitat impacted by recent (2000–2017) moderate and severe wildfire, and percent loss of habitat for the Dusky Grouse (*Dendragapus obscurus*) in the American Southwest.

<table>
<thead>
<tr>
<th>Region</th>
<th>Area of current predicted habitat (km²)</th>
<th>Area of habitat affected by wildfire (km²)</th>
<th>Loss of habitat due to wildfire (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Arizona and New Mexico</td>
<td>6694.6</td>
<td>265.3</td>
<td>4.0</td>
</tr>
<tr>
<td>Northern subregion</td>
<td>6030.2</td>
<td>140.1</td>
<td>2.3</td>
</tr>
<tr>
<td>Southern subregion</td>
<td>664.4</td>
<td>125.2</td>
<td>18.8</td>
</tr>
<tr>
<td>Gila subregion†</td>
<td>133.7</td>
<td>93.4</td>
<td>69.9</td>
</tr>
</tbody>
</table>

†The Gila subregion values are also included in the calculation of the Southern region values.

### Biogeography of the Dusky Grouse at its southern range margins

The SDM indicated that the Dusky Grouse is associated with relatively cool, mesic conditions. For instance, the most important variable in the SDM was precipitation of warmest quarter of the year, which not unexpectedly was correlated (r = 0.784) with elevation and hence reflects the adiabatic cooling and increased precipitation of increasing elevation. At the coarser 4.5-km scale of the CEM, maximum temperature of the warmest month was the most influential variable. These relationships provide independent support for the premise that populations of Dusky Grouse in the American Southwest are Pleistocene relics effectively trapped on mountaintops that have retained suitable cool, mesic climate.

Unlike most other birds, Dusky Grouse have relatively limited dispersal capabilities that may reduce or prevent movements
among mountain ranges given current climate and vegetation patterns (Zwikel and Bendell 2018). Thus, similar to other organisms with restricted dispersal capabilities such as small mammals, current distribution is likely a product of vicariance, wherein the species achieved a broader distribution during Pleistocene glacial periods but then fragmented with retraction of its range to montaintop refugia upon onset of Holocene warming (Frey et al. 2007). Therefore, limited dispersal may prevent rescue of declining populations. In such a “relaxation system” where intermontane dispersal is largely lacking, extinction becomes the overriding factor shaping contemporary distribution patterns and it results in a distribution pattern whereby only the largest patches of habitat remain occupied and populations on smaller patches have the highest extinction risk (Brown 1971). Populations may only exist in small patches of habitat if they are located near core areas or corridors exist to connect small patches of habitat to core areas (Lomolino et al. 2016). Another potential consequence of this relictual relaxation process is an erosion of genetic variation within isolated populations (Ditto and Frey 2007). Thus, the most important consideration for maintaining populations of Dusky Grouse in the American Southwest is maintaining the overall size of habitat area, with additional focus on maintaining connectivity of smaller peripheral patches of habitat.

The SDM predicted high habitat suitability of Dusky Grouse in some mountain ranges where it is not known to occur, including the Pinaleño Mountains in southeastern Arizona and the Sacramento Mountains complex in southeastern New Mexico. However, the MESS analysis indicated that at least one environmental variable in these areas was outside the range of the training data and hence predictions may be unreliable. Conversely, contemporary absence of the Dusky Grouse from these mountain ranges could be due to their biogeographic history. These ranges are highly isolated from source populations in the Rocky Mountains, and consequently have depauperate Rocky Mountain faunas (Frey et al. 2007). Absence of the Dusky Grouse from these mountain ranges is consistent with the biogeographic pattern for several terrestrial small mammals typical of the Southern Rocky Mountains such as the water shrew (Sorex navigator), southern red-backed vole (Myodes gapperi), and montane cottontail (Sylvilagus nuttallii; e.g., Frey et al. 2007).

Dusky Grouse have been translocated to five mountain ranges in the American Southwest (Appendix 9) and our SDM helps explain the fate of these translocation efforts. The only apparently successful translocation was 36 birds released to San Francisco Peaks in the 1970s. The San Francisco Peaks has a small area of high and very high habitat suitability and Dusky Grouse were reported to occur in this range historically. The only other translocation to an area where Dusky Grouse might have historically occurred, was 11 birds released to Mount Taylor in 1969. We are not aware of any observations of grouse in this range since 1979 suggesting they did not persist, despite the range containing moderate to high habitat suitability. There have been translocations to three ranges outside of the species’ historical range (Fig. 1). A total of 59 birds (of which only 13 were adults, all female) were translocated to Sierra Blanca in the Sacramento Mountains Complex from 1960 to 1963, but no grouse have been observed in this range since. Although Sierra Blanca is predicted to have very high habitat suitability, this is an area where the model cautioned interpretation because of variables outside the reference range. A total of 4 birds (1 hen and 3 chicks) were translocated to the Pinaleño Mountains in 2012, but this translocation is thought to have failed. This range has a small area ranked as very high suitability, but it also is an area where the model cautioned interpretation because of variables outside the reference range. Lastly, in 2008, 32 birds were translocated to the Mogollon Rim in Arizona in an effort to expand the distribution of the species in Arizona amid concerns of future range retractions. However, our SDM indicates that this region has low habitat suitability (< 0.3) and therefore is unlikely to support a population of Dusky Grouse. The lack of subsequent reports of grouse in this area provides further support for our model.

**Influence of climate change on Dusky Grouse in the American Southwest**

Given that climate exerts a strong control on the geographic range of Dusky Grouse within trailing-edge populations at its southern range limit, it is unsurprising that future climate change is predicted to cause a reduction in the species’ distribution. The CEM predicted substantial contractions in the geographic range of the Dusky Grouse, regardless of the region, emissions scenario, or time frame. The species is predicted to lose nearly 100% of its current high suitability habitat by the end of the 21st century under both emissions scenarios. These losses were predicted to be most rapid and severe in the southern subregion, where only moderate suitability habitat is predicted to remain in the White Mountains, Pinaleño Mountains, and Sacramento Mountains complex, although this too is predicted to be completely eliminated by the 2081–2100 time frame under the high emissions scenario. Additionally, the only large areas of suitable climate predicted to be retained in the southern subregion where Dusky Grouse are known to currently occur, is within the White Mountains, Arizona. In the Northern subregion, the Chuska (including Lukachukai) Mountains and Mount Taylor are predicted to lose their entire climate envelope under each of the
future climate scenarios, while the San Francisco Peaks are predicted to lose a large proportion of suitable climate areas under the models for the 2041–2060 time frame and are predicted to have no suitable climate by the later time period. Only the San Juan Mountains, Sangre de Cristo Mountains, and Jemez Mountains are predicted to retain a large proportion of the current climate envelope under all but the latest time frame under the high emissions scenario.

The extent of loss of suitable climate predicted by our CEM was greater than predicted in prior studies by the National Audubon Society for the combined range of the Dusky Grouse and Sooty Grouse, which predicted a range-wide 60% loss of suitable climate (National Audubon Society 2013; https://climate.audubon.org/birds/blugrs/dusky-sooty-grouse), and for the Dusky Grouse, which predicted an overall 81% loss of the species range and virtually complete loss of suitable climate from all areas of the American Southwest except the San Francisco Peaks, San Juan Mountains, and Sangre de Cristo Mountains (Wilsey et al. 2019a; https://www.audubon.org/field-guide/bird/dusky-grouse). However, the National Audubon Society models used different sources for occurrence records, spatial extent for occurrence records, methodology, and emission scenarios (National Audubon Society 2015, Wilsey et al. 2019a). Therefore, the models are not directly comparative. Regardless, each model strengthens the overriding conclusion that climate change will have profound impact to habitat for the Dusky Grouse in the American Southwest, particularly for populations in the southern subregion.

Climate change can cause deleterious impacts to wildlife on a variety of spatio-temporal scales, such as direct mortality or sublethal effects due to extreme weather events (e.g., McKechnie and Wolf 2010, Martin et al. 2017) or gradual loss of montane habitat due to upslope retraction of vegetation zones (e.g., Sekercioglu et al. 2008). Wilsey et al. (2019b) considered the chief threats of climate change to Dusky Grouse to be an increase in spring heat waves under modest warming scenarios (+1.5 °C) with the addition of weather that promotes wildfire under more severe warming scenarios (+3.0 °C). They concluded that spring heat waves could negatively affect nesting success, while wildfire could cause loss of habitat, particularly if coniferous forests fail to regenerate. However, our results suggest that recent wildfires have already caused substantial losses of habitat for Dusky Grouse in the American Southwest, particularly in the southern subregion. Singleton et al. (2019) found that the numbers, area, and severity of wildfires in Arizona and New Mexico have increased over the last three decades, with increased proportions of area burned severely in mixed coniferous forest types. In addition, they found a dramatic shift in uncharacteristic fires post-2000, which they postulated was linked to a dramatic shift to warmer and drier climate and weather (Singleton et al. 2019). Such uncharacteristic fires are projected to increase with continued climate change (Kent 2015).

Research has suggested beneficial effects of fire and other disturbances such as logging on habitat for Dusky Grouse via creating patches of early successional herbaceous or shrubby vegetation, which is necessary for successful nesting (e.g., Martinka 1972, Hutto and Patterson 2016). However, those findings were from more northern regions with extensive dense mesic coniferous forest, limited nesting habitat, and relatively small areas of disturbance, and hence are likely not relevant to the current or predicted trends for wildfires in the Southwest. In contrast, coniferous forests in the Southwest tend to be more xeric and are naturally heterogeneous and fragmented. The large size and severity of recent wildfires has eliminated a majority of the subalpine and mixed coniferous forest from some mountain ranges, such as the Mogollon Mountains in the Gila subregion. Mounting research indicates that conifers may fail to regenerate following wildfire under current and future climates, particularly in xeric environments or where repeated burns have occurred, which can result in sustained non-forest conditions (Rother and Veblen 2016, Stoddard et al. 2018). In the American Southwest, impacts of recent wildfire on Dusky Grouse habitat have been most extreme in the southern subregion eliminating majorities of subalpine and mesic mixed coniferous forest in some key regions such as the Mogollon Mountains, where the substantial loss of habitat may dramatically increase the risk of extirpation.

Given the likely metapopulation structure of Dusky Grouse in the semi-isolated mountains surrounding the Mogollon Mountains, this loss of habitat could also cause collapse of the metapopulation if the core population is no longer able to produce migrants that sustain the peripheral populations. The loss of habitat due to wildfire in the southern subregion of the Southwest are likely to continue with future climate change and provides an example of what may happen in the future to more northerly populations.

**Conservation and management implications**

Habitat for the Dusky Grouse in Arizona and New Mexico is highly fragmented such that most populations are restricted to small and isolated (or semi-isolated) mountaintop refugia, which can result in unique genetic signatures as well as heightened risk of extirpations due to habitat loss. Historical occurrence records suggest that extirpations have already occurred in some mountain ranges. However, despite the Dusky Grouse being managed as a game species, there has been little (Arizona) or no (New Mexico) published research to determine the distribution, habitat use, population sizes, demography, or other information necessary to assure sustainable populations. Recent wildfires have caused substantial loss of habitat in the southern subregion, which could jeopardize persistence of those populations. Translocations moved individuals to locations outside their natural historic range without appropriate information about the amount of available habitat or genetic makeup of source or resident birds, which can waste resources or disrupt genetic makeup. However, as trailing-edge populations may contain higher genetic diversity than populations within a species’ core range (Hunke and Petit 2005, Ferrari et al. 2018, Merker and Chandler 2020), grousé within the American Southwest may possess unique traits that could allow them to persist under future conditions. Therefore, Dusky Grouse from these areas may be viable source populations for future assisted migration efforts that seek to introduce this diversity into more northern populations that will begin to experience similar climates to those within the American Southwest in future decades.

Despite the challenges we outline for Dusky Grouse within the American Southwest, northern populations within this region (i.e., Sangre de Cristo Mountains, San Francisco Peaks) retain seemingly robust populations of grouse and may provide refugia
against moderate future climatic changes. Our future predictions do not take into account potential climate-related resiliency that may occur within populations at southern range edges (Herrero and Zamora 2014). Potential unexplored behavioral, habitat use, or genetic differences within these populations could mitigate some of the effects of a warming climate, although this needs further study. Immediate research and conservation measures are necessary to manage Dusky Grouse habitat for resiliency and to assure the long-term persistence of Dusky Grouse within Arizona and New Mexico. Research investigating the genetic health, phylogeography, and taxonomy of Southwest populations is necessary to inform conservation, especially to identify appropriate units for management. Field studies are needed to assess the current distribution, habitat use, and demography of trailing-edge Dusky Grouse populations to inform scientifically defensible management strategies, including sustainability of any harvests. Additionally, immediate attention is required to assess the conservation status of populations in southern New Mexico. Research is needed on effective translocation methods and potential for establishing climate refuges for phylogenetically distinct populations that might be at risk of extinction. Lastly, research is necessary on forest management that can promote more resilient habitat for the Dusky Grouse in the face of climate change and wildfire risk, as well as research on firefighting methods that can protect patches of habitat necessary to sustain populations of Dusky Grouse.

As this article went to press, Arizona and New Mexico were experiencing an unprecedented fire season with several megafires burning in Dusky Grouse habitat. Two of these fires in New Mexico became the largest in the state’s history. The Hermits Peak-Calf Canyon Fire started 6 April 2022 and as of 23 June 2022 had burnt > 1380 km² in the Sangre de Cristo Mountains; the fire footprint is within some of the highest suitability habitat for Dusky Grouse within the study area. The Black Fire started 13 May 2022 and as of 23 June 2022 had burnt 1316 km² in the Black Range of the Gila National Forest. Other smaller megafires burning in Dusky Grouse habitat. Two of these fires in New Mexico became the largest in the state’s history. The Hermits Peak-Calf Canyon Fire started 6 April 2022 and as of 23 June 2022 had burnt > 1380 km² in the Sangre de Cristo Mountains; the fire footprint is within some of the highest suitability habitat for Dusky Grouse within the study area. The Black Fire started 13 May 2022 and as of 23 June 2022 had burnt 1316 km² in the Black Range of the Gila National Forest. Other smaller megafires burning in Dusky Grouse habitat. Two of these fires in New Mexico became the largest in the state’s history. The Hermits Peak-Calf Canyon Fire started 6 April 2022 and as of 23 June 2022 had burnt > 1380 km² in the Sangre de Cristo Mountains; the fire footprint is within some of the highest suitability habitat for Dusky Grouse within the study area. The Black Fire started 13 May 2022 and as of 23 June 2022 had burnt 1316 km² in the Black Range of the Gila National Forest. Other smaller megafires burning in Dusky Grouse habitat. Two of these fires in New Mexico became the largest in the state’s history. The Hermits Peak-Calf Canyon Fire started 6 April 2022 and as of 23 June 2022 had burnt > 1380 km² in the Sangre de Cristo Mountains; the fire footprint is within some of the highest suitability habitat for Dusky Grouse within the study area. The Black Fire started 13 May 2022 and as of 23 June 2022 had burnt 1316 km² in the Black Range of the Gila National Forest. Other smaller megafires during this period also affected habitat on the San Francisco Mountains in Arizona and the Jemez and San Mateo Mountains in New Mexico. These fires support conclusions of this research that wildfire is outpacing the loss of habitat due to climate change within this region.

Responses to this article can be read online at: https://www.ace-eco.org/issues/responses.php/2222

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**Appendix 1.** Environmental predictor variables, descriptions, hypotheses, and predicted relationships used for the development of a species distribution model and climate envelope model for the Dusky Grouse (*Dendragapus obscurus*) in the American Southwest.

<table>
<thead>
<tr>
<th>Model</th>
<th>Environmental Variable</th>
<th>Variable Description</th>
<th>Hypothesized Function</th>
<th>Predicted Relationship</th>
<th>Citation(s)</th>
</tr>
</thead>
</table>

SDM BIO 1
Annual Mean Temperature: BIO 1 represents an annual trend in temperature and approximates total energy inputs. It is thus representative of ecosystem type.

Dusky Grouse are associated with subalpine coniferous forests (limiting winter habitat) which occur in areas with cool temperatures.


Both BIO 2
Annual Mean Diurnal Range (Mean of monthly (max temperature - minimum temperature)): BIO 2 is a measure of difference in monthly extreme high and low temperatures.

In the Southwest, Dusky Grouse occur in montane areas with relatively low temperature fluctuation compared to lower elevation sites. Coniferous forests, which are used by Dusky Grouse, do not occur in areas with high temperatures.

<table>
<thead>
<tr>
<th>Bio</th>
<th>Description</th>
<th>Notes</th>
</tr>
</thead>
<tbody>
<tr>
<td>Both</td>
<td><strong>BIO 3</strong></td>
<td>Isothermality (Mean diurnal range / temperature annual range): BIO 3 is a measure of evenness of the temperature (i.e., the daily temperature fluctuation relative to seasonal fluctuation), such as typically found in tropical or maritime environments. Dusky Grouse occur in areas where seasonal variation in temperature is greater than daily variation.</td>
</tr>
<tr>
<td>Both</td>
<td><strong>BIO 4</strong></td>
<td>Temperature Seasonality (standard deviation x 100): BIO 4 is a measure of variation in temperature across the year. Subalpine forests, which are used by Dusky Grouse, occur in areas with high temperature seasonality.</td>
</tr>
</tbody>
</table>


<table>
<thead>
<tr>
<th>Code</th>
<th>Description</th>
<th>Details</th>
<th>Source</th>
</tr>
</thead>
<tbody>
<tr>
<td>Both</td>
<td><strong>BIO 5</strong> Maximum Temperature of Warmest Month: <strong>BIO 5</strong> is the highest temperature across the year and represents a potential extreme limiting factor for many organisms.</td>
<td>Dusky Grouse are associated with cool environments and may be limited by areas with hot temperatures.</td>
<td>Bridgette et al. 2004. Weather and prairie grouse: Dealing with effects beyond our control. Wildlife Society Bulletin 32: 22–34.</td>
</tr>
<tr>
<td>Both</td>
<td><strong>BIO 7</strong> Temperature Annual Range (Maximum temperature of warmest month - minimum temperature of coldest month): <strong>BIO 7</strong> is a measure of how different the extreme coldest and warmest temperatures are across the year.</td>
<td>In the Southwest, Dusky Grouse occur in an environment with large differences in temperatures, up to a point. + sigmoidal.</td>
<td>Scherer and Diffenbaugh. 2013. Transient twenty-first century changes in daily-scale temperature extremes in the United States. Climate Dynamics 42: 1383–1404.</td>
</tr>
<tr>
<td>Both</td>
<td><strong>BIO 8</strong> Mean Temperature of Wettest Quarter: <strong>BIO 8</strong> is an index of the mean temperature during the wettest quarter of the year.</td>
<td>This period corresponds to the summer monsoon in the Southwest. Dusky Grouse are associated with subalpine coniferous forests which occur in locations that are relatively cool in the summer.</td>
<td>Peltier et al. 2016. Legacy effects of drought in the southwestern United States: A multi-species synthesis. Ecological Monographs 86: 312–326.</td>
</tr>
<tr>
<td>Climate BIO 9</td>
<td>Mean Temperature of Driest Quarter: BIO 9 is an index of the mean temperature during the driest part of the year.</td>
<td>This period generally occurs during winter in the Southwest. Dusky Grouse occur in relatively cool locations and use snow during winter for thermoregulation.</td>
<td>-</td>
</tr>
<tr>
<td>Both BIO 12</td>
<td>Annual Precipitation: BIO 12 is an index for the total precipitation in the year.</td>
<td>In the Southwest, Dusky Grouse are associated with areas of high primary productivity which is a result of high precipitation.</td>
<td>+</td>
</tr>
<tr>
<td>----------------</td>
<td>----------------------------------------------------------------------------------------------------------------</td>
<td>----------------------------------------------------------------------------------------------------------------</td>
<td>--------------------------------------------------------------------------------------------------</td>
</tr>
<tr>
<td>Climate BIO 16</td>
<td>Precipitation of Wettest Quarter: <strong>BIO 16</strong> is the amount of precipitation during the wettest quarter of the year.</td>
<td>This period occurs during the summer monsoon in the Southwest. The summer monsoon is important to producing grasses and forbs used by Dusky Grouse for nesting and foraging in summer. However, large rainfall events may cause chick mortality.</td>
<td>+ for adults, - potentially for chicks Cedarlake et al. 1982. <em>Weather conditions in early summer and their effects on September Blue Grouse (Dendragapus obscurus) harvest.</em> Great Basin Naturalist 42: 91–95. Lawson. 2018. <em>Habitat selection of Dusky Grouse on a biosolids-remediated cattle ranch in British Columbia.</em> Thesis. University of British Columbia, Vancouver, Canada.</td>
</tr>
</tbody>
</table>
| SDM | BIO 18 | Precipitation of Warmest Quarter:  
BIO 18 is the amount of precipitation in the warmest quarter of the year.  
This period reflects the summer monsoon. The summer monsoon is important to producing grasses and forbs used by Dusky Grouse for nesting and foraging in summer. | + | Comrie and Glenn. 1998. Principal components-based regionalization of precipitation regimes across the southwest United States and northern Mexico, with an application to monsoon precipitation variability. Climate Research 10: 201–215.  
| Both | BIO 19 | Precipitation of Coldest Quarter:  
BIO 19 is the amount of precipitation in the cold quarter of the year, which reflects winter snow.  
Appendix 2. Reclassification of Southwest Regional Gap Analysis Project (SWREGAP) landcover types used in the development of a species distribution model for the Dusky Grouse (*Dendragapus obscurus*) in the American Southwest.

<table>
<thead>
<tr>
<th>Landcovers Used in Analyses</th>
<th>SWREGAP Description</th>
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<tbody>
<tr>
<td>arroyo</td>
<td>S014 Inter-Mountain Basins Wash 13</td>
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<tr>
<td>arroyo</td>
<td>S020 North American Warm Desert Wash 197</td>
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<tr>
<td>aspen</td>
<td>S023 Rocky Mountain Aspen Forest and Woodland 41</td>
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<td>barren</td>
<td>N31 Barren Lands, Non-specific 247</td>
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<tr>
<td>basin/playa</td>
<td>S015 Inter-Mountain Basins Playa 7</td>
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<tr>
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<td>S021 North American Warm Desert Pavement 25</td>
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<td>S022 North American Warm Desert Playa 27</td>
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<tr>
<td>basin/playa</td>
<td>S096 Inter-Mountain Basins Greasewood Flat 189</td>
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<tr>
<td>chaparral</td>
<td>S117 Coahuilan Chaparral 99</td>
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<tr>
<td>chaparral</td>
<td>S053 Great Basin Semi-Desert Chaparral 107</td>
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<tr>
<td>chaparral</td>
<td>S057 Mogollon Chaparral 119</td>
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<tr>
<td>chaparral</td>
<td>S114 Sonora-Mojave Semi-Desert Chaparral 133</td>
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<td>desert/semidesert scrub</td>
<td>S058 Apacherian-Chihuahuan Mesquite Upland Scrub 89</td>
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<td>S062 Chihuahuan Mixed Desert and Thorn Scrub 91</td>
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<tr>
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<td>S116 Chihuahuan Mixed Salt Desert Scrub 93</td>
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<tr>
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<td>S068 Chihuahuan Stabilized Coppice Dune and Sand Flat Scrub 95</td>
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<tr>
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<td>S061 Chihuahuan Succulent Desert Scrub 97</td>
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<tr>
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<td>S059 Colorado Plateau Blackbrush-Mormon-tea Shrubland 101</td>
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<td>Plant Community</td>
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<td>-----------------</td>
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<td>S055 Great Basin Xeric Mixed Sagebrush Shrubland</td>
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<td>S054 Inter-Mountain Basins Big Sagebrush Shrubland</td>
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<td>S065 Inter-Mountain Basins Mixed Salt Desert Scrub</td>
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<td>developed</td>
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<td>D01 Disturbed, Non-specific</td>
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<td>disturbed</td>
<td>D14 Disturbed, Oil well</td>
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<td>D09 Invasive Annual and Biennial Forbland</td>
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<td>D08 Invasive Annual Grassland</td>
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subalpine conifer forest  S122 Sierra Nevada Subalpine Lodgepole Pine Forest and Woodland 81
Appendix 3. Details of occurrence records for the Dusky Grouse (Dendragapus obscurus) in Arizona and New Mexico, including references, dates, geographic coordinates, classifications of precision and reliability, and whether used in modelling.

Please click here to download file ‘appendix3.xlsx’.
Appendix 4. Map of all occurrence records for the Dusky Grouse (*Dendragapus obscurus*) in Arizona and New Mexico, excluding translocations (see Appendix 9 for details). Shaded areas are elevations > 2500 m. Black lines are state and county borders.
Appendix 5. Model validation curves for a species distribution model and current (1970–2000) climate envelope model for the Dusky Grouse (*Dendragapus obscurus*) in the American Southwest. Model metrics were calculated at each step of the variable selection process to understand how this improved model predictive power.

**Figure A5.1** Model validation curve for a species distribution model for the Dusky Grouse (*Dendragapus obscurus*) in the American Southwest.
Figure A5.2 Model validation curve for the current (1970–2000) climate envelope model for the Dusky Grouse (*Dendragapus obscurus*) in the American Southwest.
Appendix 6. Map of habitat suitability classes and multivariate environmental similarity surface (MESS) analysis for a species distribution model for the Dusky Grouse (Dendragapus obscurus) in the American Southwest.

Figure A6.1 Map of habitat suitability classes for a species distribution model for the Dusky Grouse (Dendragapus obscurus) in the American Southwest. The habitat suitability classes were based on the relative likelihood of occurrence on a logistic scale: 0-0.2 no/very low suitability (dark gray); 0.21-0.4 low suitability (light gray); 0.41-0.6 moderate suitability (green); 0.61-0.8 high suitability (yellow); 0.81-1.0 very high suitability (pink).
Figure A6.2 Results of the multivariate environmental similarity surface (MESS) analysis, which identifies areas of the species distribution model for the Dusky Grouse (*Dendragapus obscurus*) that may have unreliable predictions: (a) areas in red have one or more environmental variables outside the range present in the training data, (b) identifies the variable furthest outside its training range (deep orange-none, dark blue-Bio8, yellow-Bio2, green-Bio18, light blue=Bio14, pale orange-Bio1).

Figure A7.1 Current (1970-2000) climate envelope model of the Dusky Grouse (*Dendragapus obscurus*) in the American Southwest. Relative likelihood of occurrence of the species is represented across a continuous distribution from high likelihood (1.0-pink) to no likelihood (0-gray). Black lines are state and county borders.
Figure A7.2 Marginal response curves for the current (1970-2000) climate envelope model for the Dusky Grouse (*Dendragapus obscurus*) in the American Southwest: (a) maximum temperature of warmest month, (b) precipitation of wettest quarter, and (c) isothermality.
Figure A7.3 Map of habitat suitability classes based on the relative likelihood of occurrence on a logistic scale from the current (1970-2000) climate envelope model of the Dusky Grouse (*Dendragapus obscurus*) in the American Southwest. The habitat suitability classes were based on the relative likelihood of occurrence on a logistic scale: 0-0.2 no/very low suitability (dark gray); 0.21-0.4 low suitability (light gray); 0.41-0.6 moderate suitability (green); 0.61-0.8 high suitability (yellow); 0.81-1.0 very high suitability (pink).
Figure A7.4 Results of the multivariate environmental similarity surface (MESS) analysis of the climate envelope model for the Dusky Grouse (*Dendragapus obscurus*). Results identify areas that may have unreliable predictions: (a) areas in red have one or more environmental variables outside the range present in the training data, (b) identifies the variable furthest outside its training range (yellow-none, green-Bio5, blue-Bio3, orange-Bio16).

Figure A8.1. Map of recent (2000-2017) moderate and severe wildfires in habitat for the Dusky Grouse (*Dendragapus obscurus*) in Arizona and New Mexico. Habitat for the Dusky Grouse was defined as areas with likelihood of occurrence on logistic scale > 0.4.

Locality: Mount Graham, Pinaleño Mountains, Arizona
County: Graham
Source Population: Kaibab National Forest
Introduction Date: August 2012
Summary: One hen and three poults were released by Arizona Game and Fish Department with plans to release more in the following years. Trapping and relocation efforts ceased following this introduction, and a lack of sightings in the years since likely indicates a failed effort. Additionally, in 2018 the Frye Fire burned a large portion of the higher elevation mixed coniferous and subalpine forests needed to support this species, likely nullifying the Pinaleño Mountains for future introductions.

Reference:

Locality: Mogollon Rim, Arizona
County: Coconino
Source Population: 20 individuals from a population near Moab, Utah and 12 individuals from the north Kaibab Plateau
Introduction Date: Fall 2008
Summary: A total of 32 birds were released in the Rim Lakes Recreation Area to encourage hunting opportunities and to expand the species’ distribution within the state. There have been no subsequent credible observations suggesting that the introduction failed.

Reference:
Locality: White Mountains, New Mexico
County: Lincoln, Otero
Source Population: near Chama, Rio Arriba County, New Mexico
Introduction Date: 1960, 1961, August 1962, August 1963,
Summary: A total of 4 individuals in 1960, 9 in 1961, 36 in 1962, and 11 in 1963 were released in the Bear Canyon area of the White Mountains in south-central New Mexico. The White Mountains are part of the Sacramento Mountains complex and there are no historical records from this region despite a large area of high elevation mixed coniferous and subalpine forests. There have been no credible observations of grouse following the introduction and hence it is likely the introduction failed.
References:
New Mexico Department of Game and Fish. 1961. Annual Report. Santa Fe, New Mexico, USA.
New Mexico Department of Game and Fish. 1962. Annual Report. Santa Fe, New Mexico, USA.
New Mexico Department of Game and Fish. 1963. Annual Report. Santa Fe, New Mexico, USA.
New Mexico Department of Game and Fish. 1967. Annual Report. Santa Fe, New Mexico, USA.

Locality: Mt. Taylor, New Mexico
County: Cibola
Source Population: near Chama, Rio Arriba, New Mexico
Introduction Date: August 1969
Summary: Eleven individuals were released near La Mosca Peak in an area where grouse were known to occur previously. The last observations were made in 1978, suggesting that the relocation effort was successful for a period. However there have been no credible observations since. The current status of this population is unknown.
Reference:
New Mexico Department of Game and Fish. 1970. Annual Report. Santa Fe, New Mexico, USA.
Locality: San Francisco Peaks, Arizona
County: Coconino
Source Population: White Mountains, Arizona
Summary: A total of 5 individuals in 1975, 20 in 1976, and 11 in 1978 were released in the Bismarck Lake and Raspberry Spring areas. The historical occurrence of Dusky Grouse in the San Francisco Peaks is uncertain as historical reports were anecdotal. Recent credible observations indicate that the species still occurs in the San Francisco Peaks. Additional credible observations are available from the Kendrick Peak area suggesting that the population has expanded, if in fact it did not occur in the area prior to the introductions.

References:
Brown, D. E. 1989. Arizona game birds. The University of Arizona Press and Arizona Game and Fish Department, Tucson, Arizona, USA.