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Improving Rangeland Seedling Recruitment Using Fungicide Seed Coatings and Golden Eagle Reproductive Success in Relation to Explosive Military Tests and Trainings

Benjamin William Hoose

A thesis submitted to the faculty of
Brigham Young University
in partial fulfillment of the requirements for the degree of

Master of Science

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ABSTRACT

Improving Rangeland Seedling Recruitment Using Fungicide Seed Coatings and Golden Eagle Reproductive Success in Relation to Explosive Military Tests and Trainings

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Master of Science

The objective of the first chapter of this thesis was to determine whether fungicide seed coatings constitute an effective strategy for increasing seedling recruitment in restoration scenarios in the Intermountain West. We tested a mixture of four fungicides that address potential fungal pathogens to bluebunch wheatgrass, a dominant bunchgrass that is commonly used in restoration. Across two sites and three years, we found that the fungicide seed coating increased emergence in five of the six sites and years, with an average increase of 59.1% over the control. There was a strong interaction ($P < 0.001$) between the effects of fungicide treatment, the year and the site on emergence. This interaction was likely related to the effects of the hydrothermal microsite environment on disease severity. Further research is necessary to fully understand the conditions under which fungicide seed coatings are most likely to be effective.

The objectives the second chapter of this thesis were to 1) estimate the effects of golden eagle nest proximity to explosive disturbances on reproductive success given other relevant habitat variables (e.g. indices of topography and vegetation), and 2) determine the relative importance of nest proximity to explosive disturbances as a predictor of golden eagle reproductive success compared to other relevant habitat variables. Reproductive success data were collected from nesting territories within and surrounding land controlled and managed by the US Department of Defense. We fit the reproductive survey data using generalized linear mixed-effects models comprised of unique, hypothesis-based sets of habitat variables. We compared the models using AICc-based model selection processes. Given the best approximating model, we found no evidence that the likelihood of reproductive success was affected by nest proximity to explosive disturbances ($P = 0.460$). We further found nest proximity to explosive disturbances consistently ranked in the bottom 50% of relative variable importance. These results may indicate golden eagle tolerance or habituation to explosive military tests and trainings.

Although the two chapters of this thesis are disjointed, they are loosely unified by the ecological importance of disturbance, invasive species, and restoration within the Great Basin ecoregion.

Keywords: restoration; seed enhancement technology; seed pathology; disturbance; habituation

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CHAPTER 1

Fungicide Seed Coatings Increase Emergence of a Native Perennial Grass in the Intermountain Western United States

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ABSTRACT

The success of seed-based restoration in the Intermountain West is notoriously sporadic, with most mortality occurring between germination and emergence. Fungal pathogenesis is one process that may reduce seedling emergence and limit restoration success. This study's objective was to determine whether fungicide seed coatings constitute a cost-effective strategy for increasing emergence by reducing fungal pathogenesis and mortality. Across two sites and three years, we found that fungicide coatings increased germination by 9.0% and emergence by 59.1% on average compared to the control. The increase in emergence resulted in an estimated cost reduction of 22.4%. There was a strong interaction ($P < 0.001$) between the effects of the fungicide coating, year and site on emergence, with the effect of the fungicide ranging from a 33.7% decrease in emergence ($P = 0.042$) to a 150.9% increase in emergence ($P = 0.004$) compared to the control. The fungicide coating increased emergence compared to the control in five of the six sites and years, with the effect ranging from a 33.7% decrease ($P = 0.042$) to a 150.9% increase ($P = 0.004$). This interaction was likely related to the effect of the hydrothermal microsite environment on disease severity. Further research is necessary to fully understand the conditions under which fungicide seed coatings are most likely to be effective. Overall, these

results indicate that fungicide seed coatings have the potential to improve rangeland restoration efforts.

INTRODUCTION

Direct seeding is a tool often utilized in ecological restoration to reestablish native plant communities following disturbance or weed invasion (Erickson et al., 2017; Leger et al., 2019). Biotic and abiotic stressors commonly inhibit seeding efforts in dryland regions of the world (Aradottir & Dagmar, 2013; Svejcar et al., 2017), which commonly results in low or sporadic success, despite large expenditures (Kildisheva, Erickson, et al., 2016; Knutson et al., 2014). For many species, most of the mortality that contributes to seeding failure occurs during the critical demographic period between germination and emergence (Hardegree, Sheley, James, et al., 2020; James, Sheley, et al., 2019; James, Svejcar, & Rinella, 2011). Thus, treatments and practices that address the biotic and abiotic processes limiting survival during this demographic stage will have the greatest potential to increase the likelihood of restoration success.

Pathogenesis is one process that may limit survival of seeds and seedlings. The highest rates of disease-related mortality of plants in natural systems commonly occur during these demographic stages (Blaney & Kotanen, 2001; Gilbert, 2002). Fungi and oomycetes (henceforth referred to collectively as fungi) are particularly important contributors to seed decay and seedling disease (Fawke et al., 2015; Gilbert, 2002). Fungal pathogens may encounter and colonize seeds and seedlings via seedborne or soilborne pathways. Each pathway can simultaneously support a diversity of fungal pathogens that may interact to contribute to decay, disease, and mortality through a variety of mechanisms (Baskin & Baskin, 2014; Chambers & MacMahon, 1994; Nelson, 2018). Given the diversity of fungal pathogens on seeds and in soils, the potential for fungal pathogenesis as a limiting process to plant establishment in a restoration context is high (Lamichhane & Venturi, 2015; Nelson, 2018).

Fungal pathogenesis of seeds and seedlings is promoted by long incubation periods associated with seed dormancy (Dalling et al., 2011; Gornish et al., 2015; Kildlisheva, Dixon, et al., 2020; Nelson, 2018). Because seed dormancy is prevalent in over 80% of dryland species, fall dormant plantings are typical of dryland restoration projects (Baskin & Baskin, 2014). Planting in the fall allows seeds to overcome their dormancy requirements and be primed for emergence when conditions are favorable for plant growth in the spring (Beyers, 2004). In temperate drylands, the winter incubation period is conducive to fungal activity and growth due to the wet, cool conditions associated with snow cover (Aanderud et al., 2013; Gornish et al., 2015; Kuhnert et al., 2012). Therefore, fall-planted, dormant seeds may be exposed to high pathogen loads for 4 -5 months before emerging in the spring. The relationship between dormant seeds and pathogens has been described as a race for survival (Beckstead et al., 2007). In this scenario, seeds and pathogens are in direct competition for endosperm resources, each seeking to utilize the resources before the other. Microsite environmental factors such as soil moisture and temperature may give an advantage to either the seed or the pathogen (Allen et al., 2018). Fungal pathogenesis can also be exacerbated by abiotic stressors such as freeze-thaw cycles or drought conditions (Allen et al., 2018; Connolly & Orrock, 2015). Thus, disease severity can be largely dependent on the weather. As weather variability increases due to climate change, fungal seed decay and seedling disease may have an increasingly important effect on population dynamics of host species and on processes mediating community structure (Allen et al., 2018; Connolly & Orrock, 2015; Gilbert, 2002).

Limitations to seeding success associated with fungal seed decay and seedling disease can be addressed using fungicide seed coatings. Fungicide seed coatings may address ectophytic seed- and soil-borne diseases systemically or by creating a ‘protective zone’ surrounding the seed depending on the translocation of the fungicide (Nuyttens et al., 2013). While fungicide seed coatings are commonly used in agriculture to reduce seedling mortality and improve yield, the application of fungicides in restoration scenarios has been limited (Krupinsky et al., 2002; Munkvold, 2009; Nuyttens et al., 2013). Furthermore, seed enhancement technologies have only recently been adapted to ecological restoration (Madsen et al., 2016; Pedrini, Merritt, et al., 2017). In agriculture, fungicides are commonly applied to seeds using a film coating (Accinelli et al., 2018; Pedrini, Bhalsing, et al., 2018). The process for film coating seeds includes mixing seeds in a rotating drum while adhesives (or binders) and liquid treatments such as fertilizers, protectants, or surfactants are pumped onto a spinning disk (Accinelli et al., 2018; Madsen et al., 2016; Pedrini, Merritt, et al., 2017). This method uniformly distributes the treatment directly onto the seed. Due to the targeted nature of seed coatings, relatively small amounts of fungicide are required to produce a treatment effect, which reduces the potential of exposure of active substances to non-target organisms and increases the economic efficiency of the treatment (Munkvold, 2009; Nuyttens et al., 2013).

The purpose of this study was to determine whether seed and seedling mortality due to fungal pathogenesis on dryland restoration seedings can be mitigated by applying a fungicide seed coating. To accomplish this, we used bluebunch wheatgrass (*Pseudoroegneria spicata* (Pursh) Á. Löve), a dominant, native bunchgrass in the Intermountain West, USA, as a model species. Bluebunch wheatgrass represents an ideal model species because it is one of the most common native grasses seeded in the Intermountain West, it is well-studied, and the fungal pathogens associated with its seeds have been documented (Gornish et al., 2015). This allowed us to choose fungicides that target fungal pathogens known to be associated with bluebunch wheatgrass seeds. These include *Fusarium tricinctum*, *Fusariam solani*, *Sclerotinia homoeocarpa*, *Fusarium fujikuroi*, *Verticillium dahlia*, and *Davidiella tassiana* (Gornish et al., 2015). Bluebunch wheatgrass is typically seeded in the fall and is likely to be exposed to fungal pathogens as it is incubated in the soil over the winter in a cold, wet environment.

Our objectives were to 1) determine the effects of the fungicide seed coating on bluebunch wheatgrass germination and growth under controlled laboratory conditions, and 2) determine in the field whether fungicide seed coatings constitute a cost-effective treatment to improve rangeland seeding success. We hypothesized that the fungicide seed coating would cost-effectively increase germination and seedling emergence.

METHODS

Laboratory Trial

Seeds were coated with four fungicide products that address the pathogens identified by Gornish et al. (2015), as well as oomycete pathogens. The trade names for these products are Apron®, Dynasty®, Maxim®, and Thesis® (Syngenta, Basel, Switzerland), and the active ingredients are mefenoxam, azoxystrobin, fludioxonil, and difenoconazole, respectively (Table 1). Mefenoxam is a xylem-mobile fungicide that interferes with DNA and RNA synthesis of oomycetes. Fludioxonil is a contact fungicide that disrupts signal transduction. Azoxystrobin and difenoconazole are systemic fungicides that inhibit respiration and fungal cell wall synthesis, respectively.

Whereas most agricultural species typically emerge from the soil a few days to weeks after planting, rangeland seeds sown in the fall remain in the soil for several months and subsequently may be subject to pathogenic pressure for a longer period than their agricultural counterparts (Nelson, 2018). For this reason, and in the absence of recommended rates for rangeland applications, we chose to apply rates that were approximately 67% higher than the labeled rates designated for forage grasses or wheat. These rates remained well below the maximum allowable application rates on an active ingredient per unit area basis, assuming a seeding rate of 9.0 kg PLS ha^{-1} (Table 1).

We coated bluebunch wheatgrass seed with the fungicides using a 31-cm diameter rotary drum seed coater (Universal Coating Systems, Independence, OR, USA). We used Agrimer SCP I (Ashland Inc., Covington, KY, USA) as a binder and limestone powder ($CaCO_3$) as a filler material. Seed coating was performed on 200 g of seed, with the drum rotating at 20% of its maximum velocity. Seeds were first coated with 20 ml of a dilution comprised of the four fungicides and binder (Table 1). Directly following the application of the fungicide-binder mixture, we gradually added small amounts of limestone and binder in alternating steps, using standard seed coating techniques, until a total of 350 g of limestone powder and 128 ml of binder was applied. During the coating process, the limestone powder was delivered directly over the seed, and the binder and fungicide were applied to the spinning disk using a syringe. This technique encrusted the seed in a durable layer, maintaining the treatment in close proximity to the seed. The seed was then dried using a forced-air dryer (Braceworks Automation and Electric, Lloydminster, SK, CAN) at 43°C for approximately seven minutes.

In addition to the fungicide seed coating described above, our study included a treatment comprised of seeds coated with only binder and limestone powder (blank). The blank coating served as a procedural control to observe the effects of the coating alone without the effects of the fungicide. We also included a treatment with the seeds left uncoated (control). We tested seed germination and plant growth on these seed treatments in separate studies. For each study, we placed ten replicate samples of 25 seeds of each treatment on fine sand within 11.0 cm x 11.0 cm x 3.5 cm covered acrylic containers. All containers were watered to field capacity and placed in Precision Plant Growth Chambers (Thermo Fischer Scientific, Waltham, MA, USA) at 15°C with 12 hr light/dark cycles. Both studies were organized using a randomized complete block design using blocks to account for positional variability within the incubator. The position of the blocks and experimental units within blocks were rearranged twice a week throughout the studies.

For the germination study, we recorded the number of seeds with a radicle exceeding 2 mm in length every 2 – 4 d for 31 d. Seeds that had germinated were removed from the container at the time of counting. From the germination data, we estimated the time to reach 50% germination (T_{50}), and final germination percentage (FGP) using non-linear, three-parameter log-logistic time-to-event models (Ritz, Pipper, & Streibig, 2013). Time-to-event models were fit using the 'drm' function of the 'drc' package (Ritz, Baty, et al., 2015) in program R (R Core Team, 2019). We compared treatment effects using a Bonferroni pairwise comparison test (α = 0.05).

In the biomass study, plants were allowed to grow for 31 d and then harvested. Plants were harvested by washing the sand from the roots and drying the plants at 105ºC for three days. After drying, root biomass and shoot biomass were measured separately. We analyzed total biomass and the root-to-shoot ratio using linear mixed-effects models, with blocks included as a random effect. We compared the results for each treatment using a Bonferroni pairwise comparison test ($\alpha = 0.05$).

Field Trial

We conducted field experiments at two sites near Lookout Pass and Santaquin, Utah to determine the effects of the fungicide coating on germination and emergence under field conditions. The Lookout Pass site (40.139003, -112.507367) is located in Tooele County, east of the Onaqui Mountains and approximately 8 km northwest of Vernon, UT. The elevation of the site is 1685 m, the slope is 3.0%, and the soil pH is approximately 8.2 (Soil Survey Staff, 2019). The site is characterized as a semi-desert gravelly loam Wyoming big sagebrush (*Artemisia tridentata* Nutt. ssp. *wyomingensis* [Beetle & A. Young] S. L. Welsh) site but is currently dominated by crested wheatgrass (*Agropyron cristatum* (L.) Gaertn.). Lookout Pass receives an average of 287 mm of precipitation per year, mostly in the form of snow. The Santaquin site (39.907287, -111.816306) is located in Juab County, approximately 16 km south of Santaquin, UT. The elevation of the site is 1561 m, the slope is 7.2%, and the soil pH is approximately 7.6 (Soil Survey Staff, 2019). The site is characterized as a mountain gravelly loam, mountain big sagebrush site (Utah Division of Wildlife Resources Range Trend Study Site, 2020) and is currently dominated by bulbous bluegrass (*Poa bulbosa* L.), field bindweed (*Convolvulus arvensis* L.), jointed goatgrass (*Aegilops cylindrical* Host) and cheatgrass (*Bromus tectorum* L.). The Santaquin site receives an average of 481 mm of precipitation per year, mostly in the form of snow (Soil Survey Staff, 2019). In preparation for seeding, both sites were sprayed in April of the previous year and two weeks prior to planting, with 280 g ai · ha^{-1} of glyphosate (Accord Concentrate®, Dow AgroSciences, Indianapolis, IN, USA). Plant material that was not killed by the herbicide was removed by hand on the day seeds were sown. Both sites were surrounded by a fence designed to exclude livestock and wildlife, including lagomorphs and rodents.

Soil moisture and temperature was measured in a central location at each site using two MPS-6 water potential sensors (METER, Pullman, WA) that were buried 1 cm below the soil surface. Daily average soil temperature and water potential was calculated to compare relative differences between sites. Long-term and monthly averages of precipitation and ambient temperatures were also derived from models produced by PRISM's (Parameter-elevation Regressions on Independent Slopes Model) Oregon Climate Service (PRISM Climate Group 2020). The long-term averages were taken from 1981-2010.

We organized the field germination and emergence experiment following a randomized complete block split-plot design with sites and years comprising the whole plots and blocks comprising the subplots. Blocks contained three seed treatments: control, blank, and fungicide coated seed sown in separate rows. The study was implemented over three years, from 2016-2018, with seeds sown each year between October 20 and November 3. We modified some aspects of the study design following the 2016 planting season due to the preliminary nature of that portion of the study. In 2016, seeds were planted in 3 m rows, whereas in 2017 and 2018, seeds were planted in 1.5 m rows within 15 cm deep furrows. We used furrows to moderate microsite temperature and water potential, which reduces the variability caused by weather (Anderson et al., *In review*).

In 2016, seeds were coated following the same procedure as the laboratory study. However, in 2017 and 2018, we replaced Thesis® in the fungicide coating with Dividend® because Thesis® was discontinued by Syngenta. Like Thesis®, the primary active ingredient of Dividend® is difenoconazole, but Dividend® also contains a small amount of mefenoxam. We also modified the binder used from Agrimer SCP I in 2016, to Agrimer SCP II (Ashland Inc., Covington, KY, USA) in 2017 and 2018, which improved the stability of the coating.

To evaluate germination response to the treatments, we planted mesh bags (SumDirect ®, Dongguan Fuxin Electronics Co Ltd, Henglitown, Guangdong, CHN), henceforth germination bags, that each contained seeds of a single treatment and sieved soil that was collected from the site in which the bag was planted (Abbott & Roundy, 2003). In 2016, we buried germination bags in individual rows in five blocks, while in 2017 and 2018, we buried germination bags in individual rows in ten blocks. In 2016, each germination bag contained 25 seeds, while in 2017 and 2018, each germination bag contained 40 seeds. Germination bags were harvested each year in March. In the laboratory, we separated the seeds from the soil by lightly washing the contents of the bag over a fine mesh screen. Seeds were considered germinated when the radicle exceeded 2 mm. We evaluated the emergence treatment response by sowing seeds of each treatment in rows organized in ten blocks at a rate of 82 PLS m^{-1}. We counted emergence in April of each year.

We evaluated the effect of fungicide seed coatings on the proportion of germinated and emerged seedlings using generalized linear mixed-effects models with a binomial response distribution (Sileshi, 2012). Following this modelling structure, individual seeds comprised the experimental units. Because seeds were grouped in germination bags for germination tests and rows for emergence tests, germination bags and rows were included in the models as random effects. Block and year were also defined as random effects with germination bags and rows implicitly nested within blocks, and blocks implicitly nested within sites and years. Treatments and sites were defined as fixed effects.

The significance of all two and three-way interactions between treatment, site, and the year was tested by comparing models with and without individual interaction terms using likelihood ratio tests. Due to significant interactions, we also fit models of each year and site separately. All analyses were performed using R statistical software (R Core Team, 2019).

Cost Analysis

We tested the economic viability of fungicide seed coatings by comparing the estimated cost to produce 1,000 seedlings on the landscape using fungicide coated seed and the control. We assumed bluebunch wheatgrass cost \$12.24 kg^{-1} of pure live seed (PLS) and that there were 308,647 seeds kg^{-1} PLS. These values were based on personal communications with the Utah Division of Wildlife Resources Great Basin Research Center and Seed Warehouse (Ephraim, UT, USA). We estimated the cost of fungicide coatings adding the estimated costs of materials and seed coating per kilogram of PLS at the industrial scale (Table 2). These values reflect personal communications with Syngenta and Summitt Seed Coatings (Caldwell, ID, USA). We divided the cost of control and fungicide coated seed by the respective average percent emergence using the results from our study. This result was multiplied by 1,000 to represent the cost to produce 1,000 seedlings on the landscape for interpretability.

RESULTS

Laboratory Trial

The FGP estimates of the control, blank, and fungicide treatments were 79.8 ± 2.7%, 85.6 ± 3.0%, and 88.3 ± 3.1% respectively, with no significant differences between them ($P > 0.050$;

Table 3). Both the fungicide and the blank coatings slowed germination, with T_{50} estimates 1.93 ± 0.64 d ($P = 0.007$) and 1.99 ± 0.59 d ($P = 0.002$) greater than the control (17.59 ± 0.34 d), respectively (Table 3). The fungicide coating increased seedling biomass over the control by 40.7 ± 13.3% ($P = 0.020$), and the blank by 29.4 ± 12.2% ($P = 0.082$; Table 3). The root-to-shoot ratios of the control, blank, and fungicide coatings were 1.27 ± 0.18, 1.37 ± 0.20, and 1.63 ± 0.25, respectively, with no significant differences between them ($P > 0.050$; Table 3).

Field Trial

Santaquin and Lookout Pass experienced higher than normal precipitation during the seed incubation period (i.e. October through May) in 2016 and 2018, but lower than normal precipitation in 2017 compared to long-term averages (Fig. 1-1). At Lookout Pass in 2017, soil conditions were exceptionally dry compared to other sites and years with 64% of the incubation period characterized by water potentials below -1.5 MPa (Fig. 1-2). By contrast, more than 80% of the incubation period was characterized by soil water potentials above -1.5 MPa in the remaining sites and years (Fig. 1-2). Soil water potential was also more variable in Lookout Pass in 2017 compared to the other sites and years (Fig. 1-2). Temperatures at both sites were generally similar to the long-term averages although both sites experienced slight warm spikes in January of 2018 (Fig. 1-1). On average, soil moisture was generally considerably higher in Santaquin than Lookout Pass, but temperatures were fairly similar between sites (Fig. 1-1 and 1-2).

Across all sites and years, the average germination percentages for the control, blank, and fungicide treatments were 79.0 ± 1.0%, 78.8 ± 1.0%, and 86.1 ± 0.8%, respectively (Fig. 1-3). We identified interactions between the year and the treatment ($P < 0.001$) and the year and the site ($P < 0.001$), which complicated meaningful interpretation of treatment effects across all sites and years. The fungicide coating increased germination compared to the control in three of the six (50.0%) sites and years with effects ranging from a 2.5% decrease in germination (Lookout Pass 2017; $P = 0.753$) to a 25.2% increase in germination (Lookout Pass 2018; $P < 0.001$; Fig. 1-3). The blank performed similarly to the control in all sites and years (Fig. 1-3).

Across all sites and years, the average emergence percentages for the control, blank, and fungicide treatments were 14.9 ± 0.3%, 15.9 ± 0.4%, and 23.7 ± 0.4%, respectively (Fig. 1-3). We identified a significant three-way interaction between the treatment, the site, and the year ($P < 0.001$). The fungicide coating increased emergence compared to the control in five of the six (83.3%) sites and years with effects ranging from a 33.7% decrease in emergence (Lookout Pass 2017; $P = 0.042$) to a 150.9% increase in emergence (Santaquin 2016; $P = 0.004$; Fig. 1-3). The effect of the blank coating varied considerably by site and year, as it performed similarly to the control in four of the six (66.7%) sites and years and similarly to the fungicide coating in three of the six (50.0%) sites and years (Fig. 1-3). Notably, in Lookout Pass in 2017, the blank coating and the fungicide coating decreased emergence compared to the control but were similar to each other (Fig. 1-3).

Cost Analysis

The commercial costs of control seed and fungicide coated seed were approximately \$12.24 kg^{-1} PLS and \$15.04 kg^{-1} PLS, respectively. Thus, the fungicide coating increased direct costs by approximately 22.9%. However, on average 14.9% of control seeds emerged, compared to 23.7% of fungicide coated seeds. Thus, on average, the fungicide coating increased the probability of emergence by an average of 59.1% under the study conditions. This resulted in costs of $0.265 and $0.206 per 1,000 seedlings for the control and fungicide coated seed, respectively, with the fungicide reducing cost by 22.4%. Dividing the analysis by site, the fungicide coating decreased the cost per 1,000 seedlings by 28.9% in Santaquin and 13.5% in Lookout Pass.

DISCUSSION

The success of seed-based restoration efforts in dryland settings largely depends on the critical demographic period between germination and emergence (Hardegree, Sheley, James, et al., 2020; James, Sheley, et al., 2019; James, Svejcar, & Rinella, 2011). We hypothesized that fungal seed and seedling pathogenesis contribute to this bottleneck and that fungicide seed coatings would increase emergence by reducing fungal pathogenesis. Across two sites and three years we found that most seeds germinated (81.3% on average) but relatively few emerged (18.2% on average), which confirmed a strong emergence bottleneck in our study. We further found that fungicide seed coatings substantially increased emergence, but relatively negligibly increased germination (Fig. 1-3). This disparity in effect size supports our hypothesis that fungal pathogens contributed to the emergence bottleneck. The fungicide coating increased emergence in five of the six sites and years, by 59.1% on average, which supports our hypothesis that fungicide seed coatings would constitute an effective strategy for increasing emergence. Furthermore, our cost analysis indicated that fungicide seed coatings were cost-effective under the study conditions.

The effect of the fungicide coating on emergence was highly dependent on the year and site, as indicated by strong interaction terms (Fig. 1-3). It is likely that these interacting effects were largely attributable to differences in microsite conditions as influenced by such factors as weather, soils, and microbial community dynamics (Blaney et al., 2001; Connolly & Orrock, 2015; Elhert et al., 2014; Hardegree, Sheley, Duke, et al., 2016; Hardegree, Sheley, James, et al., 2020; Lamichhane et al., 2018). One way that weather could influence seed and seedling disease severity is by affecting germination timing and growth of both plants and pathogens (Allen et al., 2018; Lamichhane et al., 2018; Hardegree, Sheley, James, et al., 2020). Germination and growth rates of plants and fungal pathogens are proportional to the amount that temperature and water potential exceed a threshold value (Allen et al., 2018; Barth et al., 2015; Bradford, 2002; Hardegree, Roundy, et al., 2018). Because threshold values and response rates are diverse and unique to individual species, it is likely that seeds and pathogens respond differently to microsite temperature and water potential (Allen et al., 2018; Lamichhane et al., 2018; Richardson et al., 2018; Hardegree, Sheley, James, et al., 2020). Following the race for survival model for seed pathogenesis, the relative responses of seeds and pathogens to the hydrothermal environment regulate processes of pathogenesis and escape (Beckstead et al., 2007). The hydrothermal environment in small windows of time may favor fungal growth and pathogenesis or seed germination, growth, and escape, thereby driving disease severity and the observed interactions (Allen et al., 2018; Franke et al., 2014).

The microsite hydrothermal environment's impact on seed and seedling disease severity is further complicated by microbial community dynamics. Multiple species of graminoid pathogens are associated with bluebunch wheatgrass seed under field conditions, each of which may or may not be pathogenic to bluebunch wheatgrass (Gornish et al., 2015). Thus, it is likely that the pathogenesis of bluebunch wheatgrass seed and seedlings is not a monospecific process, but rather a process involving a community of microbes, some of which may form synergistic relationships (e.g. commensal-pathogen or pathogen-pathogen) affecting disease severity

(Lamicchane et al., 2018; Lamichhane & Venturi, 2015). Such systems, appropriately termed disease complexes, are common in wildland settings (Lamicchane & Venturi, 2015). Microbial communities and disease complexes can be highly sensitive to the hydrothermal environment and other stochastic ecological processes (Aanderud et al., 2013; Lamichhane et al., 2018; Lamichhane & Venturi, 2015). Thus, the compositions of disease complexes affecting seeds and seedlings in this study were likely unique to each site and year to some degree. It follows that the dynamics of the microsite microbial community and disease complex could have drastically affected disease severity and the treatment interactions observed in this study.

One of the most apparent sources of the strong interaction between the site, year, and treatment on emergence was that both the blank and the fungicide coatings produced lower emergence than the control but similar results to each other in Lookout Pass in 2017 (Fig. 1-3). This pattern was unique to Lookout Pass in 2017 and was correlated with extraordinarily low water potentials during the winter relative to the other sites and years (Fig. 1-2 and 1-3). With the exception of Lookout Pass in 2017, all sites and years maintained soil water potentials greater than -1.5 MPa for more than 80% of the winter incubation period. By contrast, 64% of the winter incubation period was characterized by soil water potentials below -1.5 MPa in Lookout Pass in 2017 (Fig. 1-2). Furthermore, Lookout Pass in 2017 experienced extreme fluctuations in water potential during the winter months compared to the other sites and years (Fig. 1-2). The dry and variable soil conditions of Lookout Pass in 2017 were likely a result of abnormally low precipitation, as compared to the 30-year normal, in October through January (Fig. 1-1). Because the blank and the fungicide treatments performed similarly, we infer that the deleterious treatment effect was due to their common thick coating. As was demonstrated in the laboratory trial, the seed coating slowed germination. This was likely due to an increased water potential threshold required for imbibition. Assuming the delay in germination caused by the seed coating was a function of imbibition, the effect of the coating would have been exacerbated by the exceptionally dry conditions in Lookout Pass in 2017. Such a delay in germination could have extended emergence past our count date (Boyd & James, 2013).

Although germination timing may explain the deleterious effect of the seed coating on emergence in Lookout Pass in 2017, it fails to explain why the fungicide coating did not compensate for the reduced emergence by increasing survival compared to the blank coating. This lack of a positive treatment effect suggests that fungal pathogenesis was not a strong limiting factor to seedling emergence in Lookout Pass in 2017. The exceptionally dry conditions in Lookout Pass in 2017 may have reduced disease severity by impeding growth and pathogenesis of the most important disease complexes at a higher rate than the growth and escape mechanisms of bluebunch wheatgrass through a variety of individual and community scale mechanisms (Lamichhane & Venturi, 2015; Lamichhane et al., 2018). Such interactions between the microsite hydrothermal environment and microbial community dynamics and processes are highly complex. Further research is necessary to fully understand how these interactions influence seed and seedling disease severity, plant phenology, and restoration success. Additional research is also necessary to integrate these concepts into the context of a changing climate (Connolly & Orrock, 2015; Lamicchane et al., 2018).

Based on emergence counts, the fungicide seed coating reduced restoration costs by approximately 22.4% on average. Assuming the sites and years of this study are representative of the Intermountain West, this reduction in cost could be emulated in the field if land managers apply fungicide seed coatings and reduce the seeding rate by 37.1% to reflect the average increase in emergence (59.1%) produced by the fungicide. Following the same assumption of representativeness, fungicide coatings would not be cost-effective in every setting, but long-term averages would result in net savings. Although this study involved only two sites and three years, and therefore is not fully representative of the diverse restoration scenarios in the Intermountain West, it provides strong evidence that fungicide seed coatings have the potential to cost-effectively improve restoration success. Future research is merited to explore the use of fungicides in other settings, particularly post-fire or other disturbances.

In order for fungicide seed coatings to be widely adopted for restoration use, they must first be registered for such use under the Environmental Protection Act (EPA). This process would include a thorough investigation of the risks of fungicide use to humans, wildlife, fish, plants, and other non-target organisms, as well as surface and ground water contamination in a variety of restoration contexts. Although these risks were investigated prior to registration for agricultural use, some risks may be of higher concern in restoration settings. For example, the risk of fungicides to beneficial microorganisms, particularly mycorrhizae, are likely more important when seeding perennial restoration species that will experience summer drought than when seeding annual agricultural species that do not experience consistent summer drought. The effects of fungicide seed coatings on mycorrhizae are diverse, understudied, and complicated by a myriad of variables including the mobility and mode of action of fungicide, the plant species, the microbial community, and their interactions (Cameron et al., 2017). However, non-target effects may be mitigated by the highly localized nature of seed coatings and the short half-lives of most fungicides relative to the incubation period of fall-planted restoration species (Cameron et al., 2017; Jin et al., 2013; Table 1). We encourage collaboration between researchers, government agencies, and private seed treatment companies to investigate non-target effects of fungicide seed coatings and register fungicides for restoration use if appropriate.

CONCLUSION

Using bluebunch wheatgrass as a model species, we demonstrated that fungicide seed coatings have the potential to cost-effectively improve the probability of emergence in dryland restoration seedings. The success of fungicide seed coatings in our study and agriculture provide promising evidence that fungicides may be used to improve seeding success in a variety of restoration scenarios. Future research should explore the effects of fungicide seed coatings on other species and in other biomes where fungal pathogenesis is limiting restoration success. Further research should also explore the interrelated concepts of hydrothermal accumulation, the race for survival, and disease complexes as these may drive disease severity. Exploring the effects of fungicides over a larger sample of species and sites and understanding the ecological processes driving interactions would allow for a higher degree of inference and improve our ability to determine the conditions under which fungicides are likely to be cost-effective.

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FIGURES

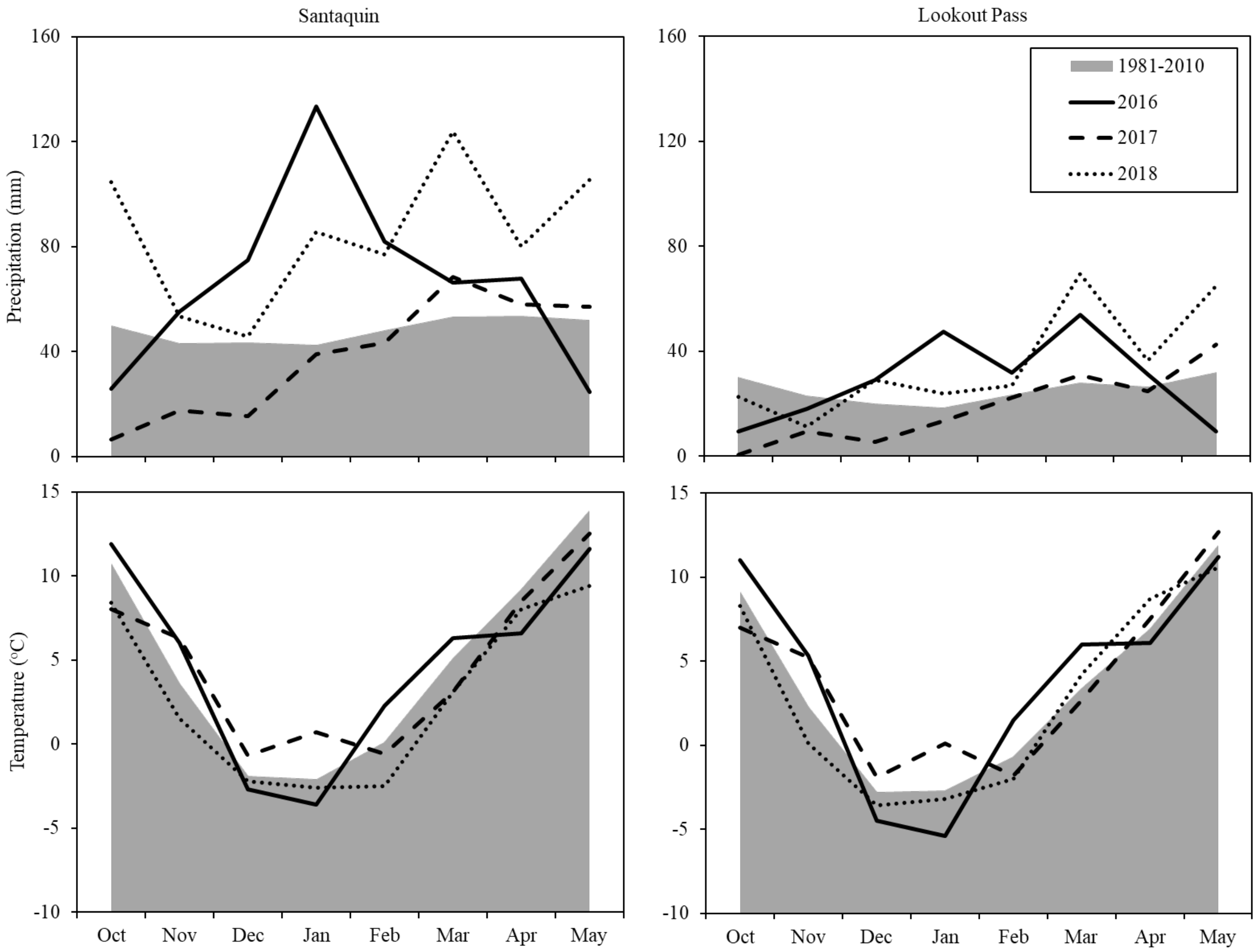

Figure 1-1. Monthly average precipitation and temperature between planting and emergence at each site and year compared with the 30-year average.

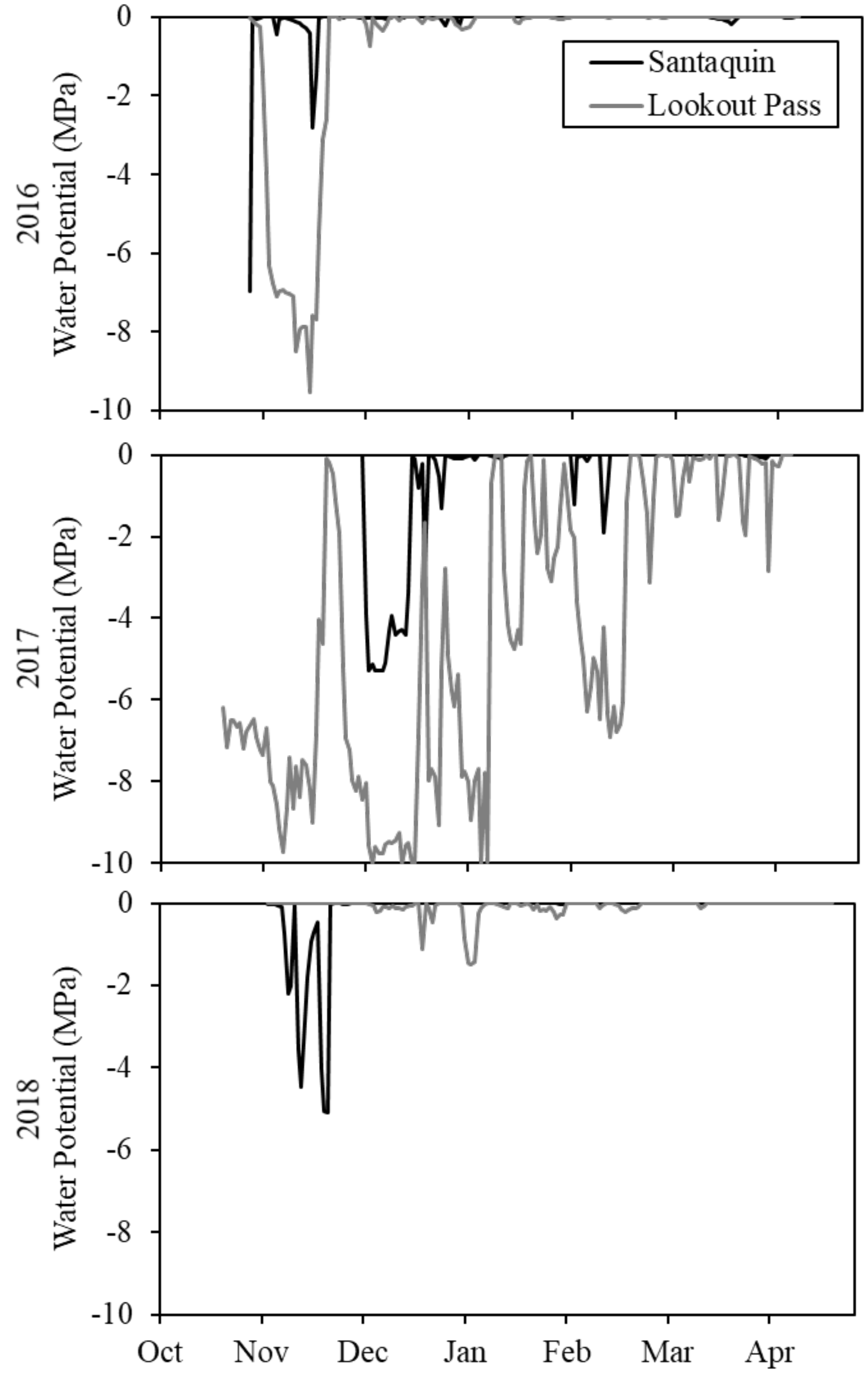

Figure 1-2. Daily average water potential 2 cm below the surface between planting and emergence at each site and year.

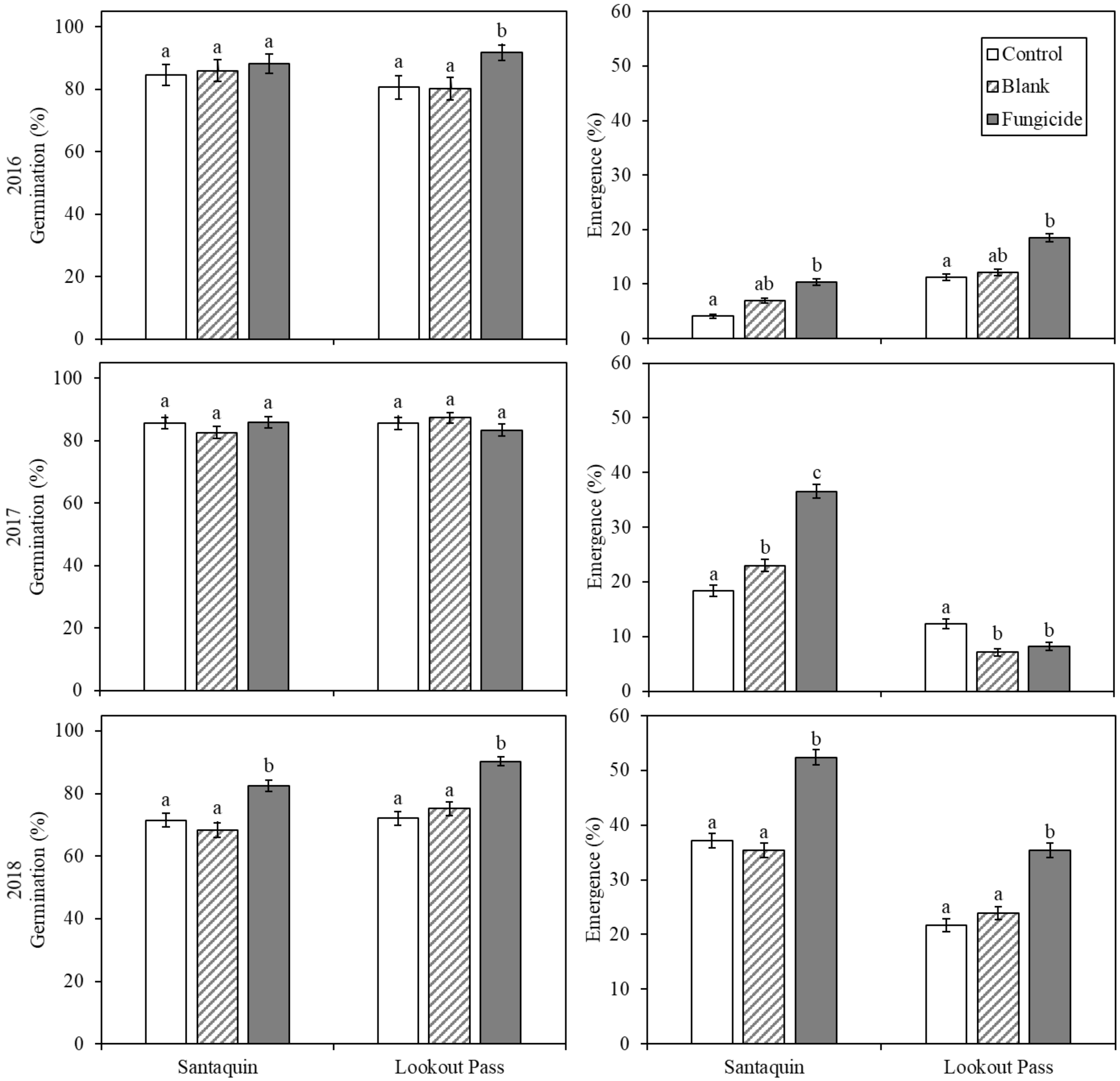

Figure 1-3. Average percentages of germination and emergence across all treatments, sites, and years. Error bars represent the standard error and letters represent significant differences ($P < 0.05$).

TABLES

Table 1-1. The characteristics of the fungicides applied to bluebunch wheatgrass via seed coating and the corresponding active ingredients. The applied rates are 167% of the labeled rates for similar agricultural species. The half-lives represent averages under field conditions. The applied rates ha^{-1} assume a seeding rate of 9.0 kg PLS ha^{-1}.

Fungicide trade name	Active ingredient	Pathogens addressed	Half-life (d)	Applied rate ($mg_{fungicide}/g_{seed}$)	Applied rate ($g_{a.i.}$/ha)
Apron XL®	mefenoxam	oomycetes (e.g. *Pythium*)	70	0.775	2.388
Maxim 4FS®	fludioxonil	broad spectrum (e.g. *Fusariam, Verticilium*)	69	0.207	0.747
Dynasty®	azoxystrobin	broad spectrum (e.g. *Pythium, Fusariam*)	14	1.195	1.029
Thesis®	difenoconazole	broad spectrum (e.g. *Fusarium, Verticilium*)	120	0.427	0.296

Table 1-2. An itemized summary of the estimated costs of producing fungicide-coated seed for researchers and commercial applications.

	Seed coating costs ($/kg$_{seed}$)	
Item	Research	Commercial
Apron XL®	$0.77	$0.42
Maxim FS®	$0.20	$0.11
Thesis®	$1.19	$0.60
Dynasty®	$0.42	$0.24
Binder	$3.79	$0.55
Ca. carbonate	$0.11	$0.11
Seed coating	$0.77	$0.77
Total cost	$7.28	$2.80

Table 1-3. A summary of pairwise comparisons between treatments for each response in the laboratory trials. P-values were adjusted for multiple comparisons using the Bonferroni method.

Response	Pairwise Comparison	Difference	Standard Error	*P*
Final Germination Percentage (%)	Control - Blank	-5.80	4.02	0.450
	Control - Fungicide	-8.50	4.11	0.114
	Blank - Fungicide	-2.73	4.32	0.999
Time to 50% Germination (d)	Control - Blank	-1.99	0.593	0.002
	Control - Fungicide	-1.93	0.638	0.007
	Blank - Fungicide	0.062	0.722	0.999
Biomass (g)	Control - Blank	-0.004	0.007	0.999
	Control - Fungicide	-0.022	0.007	0.020
	Blank - Fungicide	-0.017	0.007	0.082
Root-Shoot Ratio	Control - Blank	-0.109	0.181	0.999
	Control - Fungicide	-0.365	0.181	0.176
	Blank - Fungicide	-0.256	0.181	0.520

CHAPTER 2

Golden Eagle (*Aquila chrysaetos*) Reproductive Success Relative to Explosive Military Tests and Trainings

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ABSTRACT

Golden Eagles (*Aquila chrysaetos*) are a species of conservation concern in the western United States. Military tests and trainings may constitute a threat to Golden Eagle population stability in areas where explosive disturbances could reduce reproductive success. The objectives of this study were to 1) estimate the effects of nest proximity to explosive test and training areas (target areas) on Golden Eagle reproductive success given other relevant habitat variables, and 2) determine the relative importance of nest proximity to target areas as a predictor of Golden Eagle reproductive success compared to other relevant habitat variables. To accomplish this, we fit multiple generalized linear mixed effects models, comprised of unique combinations of habitat variables, to reproductive success survey data collected within and surrounding land controlled and managed by the US Department of Defense. Models were then compared within separate information-based model selection processes. We found no evidence that the likelihood of reproductive success was affected by nest proximity to target areas ($P = 0.460$) and that nest proximity to target areas consistently ranked in the bottom 50% of relative variable importance. These findings may indicate Golden Eagle tolerance or habituation to explosive military tests and trainings. Golden Eagle conservation on military lands may be best enhanced by improving

prey habitat, mitigating nest exposure, and maintaining isolation of disturbances to areas of least environmental impact.

INTRODUCTION

Golden Eagles (*Aquila chrysaetos*) are an iconic species of conservation concern in the United States of America (U.S. Fish and Wildlife Service [USFWS] 2008). Historic population declines and enduring conservation interest have afforded Golden Eagles continued federal protection under both the Migratory Birds Treaty Act (16 U.S.C. 703–712) and the Bald and Golden Eagle Protection Act (16 U.S.C. 668-668d). The principle objective of the Bald and Golden Eagle Protection Act is to maintain “stable or increasing populations” of both species (USFWS 2016). Although Golden Eagle populations are generally considered to be stable in the western United States (Millsap et al. 2013), populations may be declining on a localized level, particularly in the Great Basin Ecoregion (Kochert & Steenhof 2002, Slater et al. 2013). Furthermore, even stable populations of Golden Eagles may be susceptible to population decline due to low reproductive potential (Nielson et al. 2016).

One threat to Golden Eagle population stability is anthropogenic disturbance (Lindenmayer et al. 2016; Pauli et al. 2017). Disturbance may be defined as any activity that alters the normal physiology or behavior of an animal during critical life functions, such as habitat selection, nesting, and brood rearing (Battisti 2016). Golden Eagles may respond to disturbance by altering foraging flight and perching (Schueck et al. 2001; D’Acunto et al. 2018), expanding or shifting home ranges (Schueck et al. 2001), switching nests within a territory (Watson 2010), avoiding nest sites that are otherwise optimal (Sih et al. 2011; Carlisle et al. 2018), or, by contrast, returning to nest sites that have become suboptimal due to disturbance (Kochert et al. 1999;

Chalfoun & Schmidt 2012). Nesting Golden Eagles may respond to disturbance by increasing vigilance, flushing, or abandoning the nest (Grubb et al. 2010; Watson 2010; Spaul & Heath 2017). Any of these behaviors could incur reproductive costs either indirectly, through reduced energy budgets or diversion of resources from parental care (Pauli et al. 2017; Carlisle et al. 2018), or directly as adults leave nestlings exposed to inclement weather, predation and kleptoparasitism (Camp et al. 1997; Schueck et al. 2001; Simes et al. 2017). Responses to disturbance could be exacerbated or mitigated by vegetation cover, topographical structures, local population density and distribution, habituation, and type, severity, timing, duration, frequency, and proximity of the source of disturbance (Camp et al. 1997; Rankin et al. 2009; Grubb et al. 2010). Likewise, the effect of disturbance on reproductive success could interact with abiotic and biotic stressors such as land use change (Kochert & Steenhof 2002; Preston et al. 2017; White et al. 2018), climate change (Tack et al. 2017; Kochert et al. 2019), invasive species (Slater et al. 2013; Tack et al. 2017), and altered fire regimes (Kochert & Steenhof 2002; Slater et al. 2013).

One source of disturbance within Golden Eagle nesting habitat in the western United States is military testing and training (Schueck et al. 2001; Slater et al. 2013). Despite characteristically high levels of disturbance, military lands generally offer unique conservation opportunities (Stein et al. 2008). In the United States, the Readiness and Environmental Protection Integration (REPI) program stipulates that goals of military readiness be integrated with goals of environmental conservation, thereby reconciling competing interests (Hanson 2018). A fundamental and implicit component of the mission of REPI is quantifying the impacts of military training on species of conservation concern, including Golden Eagles (Slater et al. 2013; Lindenmayer et al. 2016).

The Utah Test and Training Range (UTTR) is one military area in the western United States that sustains a breeding population of Golden Eagles. The UTTR, managed by Hill Air Force Base, UT, is designated for training in air-to-air combat, air-to-ground inert and live practice bombing, and gunnery training. Explosive tests and training exercises are constrained to designated target areas. Thus, target areas represent sources of repeated explosive disturbance. Although tests and trainings are not likely to directly harm Golden Eagles because nest sites on the range are strictly protected in accordance with REPI, repeated explosive disturbance is likely to elicit negative behavioral responses (Schueck et al. 2001; Rankin et al. 2009; Grubb et al. 2010). Severe behavioral responses, particularly during nesting, incubation, and brood rearing, could result in reduced Golden Eagle population density and reproductive success near the source of the disturbance. Understanding the effects of these disturbances on Golden Eagle reproductive success is critical for maintaining their populations on military test and training ranges.

Because the effects of explosive tests and trainings on Golden Eagle reproductive success may interact with other habitat components, it is important to quantify the effects of the disturbance holistically. Furthermore, Golden Eagles may be best conserved by addressing the most limiting factors to reproductive success. Thus, both the effect of disturbance given other relevant habitat components and the relative importance of disturbance compared to other habitat components are of conservation interest. Following this logic, the objectives of this study were to: 1) estimate the effect of nesting territory proximity to target areas on Golden Eagle reproductive success given other relevant variables, and 2) determine the relative importance of nesting territory proximity to target areas as a predictor of Golden Eagle reproductive success compared to other relevant variables. We hypothesized that nesting territories nearer to target areas would exhibit lower reproductive success on average and that nesting territory proximity to target areas would be a relatively important variable in predicting Golden Eagle reproductive success.

METHODS

Study Area

The UTTR is a 2,624 square-mile area in western Utah, comprised of a North Range and South Range (Fig. 2-1). The two ranges are separated by a buffer that surrounds I-80. In addition to the North and South Ranges, the study area included a portion of the Grassy Mountains within 4 km of the southeast border of the North Range. The UTTR has been in use since 1940; however, the munitions and missile testing facilities were not constructed until 1964. There are 28 designated target areas within the UTTR with varying degrees of use and disturbance. There are 17 known Golden Eagle nesting territories in the study area. Nesting territories range from existing within target area boundaries to 6.9 km from target areas.

The UTTR is characterized as a cold desert and receives an average of 36.3 cm of precipitation a year, much of which is in the form of snow (PRISM 2020). The long-term monthly average low and high temperatures are -7.9 and 31.2 ºC, respectively (PRISM 2020). Guzzlers provide the majority of free water within the study area. The major landcover types of the UTTR include salt flats (84.6%), shrublands (11.7%), and grasslands (3.1%) (LANDFIRE 2014). Salt flats are mostly devoid of vegetation except for scattered populations of pickleweed (*Allenrolfea occidentalis*). Shrublands are dominated by greasewood (*Sarcobatus vermiculatus*) and shadscale (*Atriplex confertifolia*), although some isolated sagebrush (*Artemisia tridentata*) patches exist within the study area. Grasslands are dominated by cheatgrass (*Bromus tectorum*), with a few mixed crested wheatgrass (*Agropyron cristatum*) and Siberian wheatgrass (*Agropyron fragile*) stands. Utah juniper (*Juniperus osteosperma*) stands are few and isolated.

Field Methods

Nest-site surveys were conducted through the cooperative efforts of the United States Department of Defense (DOD), the Fish and Wildlife Service (USFWS), the Bureau of Land Management (BLM), the Utah Division of Wildlife Resources (UDWR), Hawkwatch International, and the Raptor Inventory Nest Survey (RINS) beginning in 1976 (Slater et al. 2017). Nests were located by scanning cliffs and rocky outcroppings on hills using binoculars or spotting scopes (Slater et al. 2017). Nesting territories were surveyed between mid-March and early July in 2006, 2012, 2013, and 2015-2018 to document occupancy, and during May or June in the same years to document reproductive success. Nesting territories were defined as 'occupied' when two breeding-age eagles were present within the territory or when one adult was present and exhibited territorial or reproductive behavior (Slater et al. 2017). Territorial behavior was defined as aggressively chasing other individuals away from the territory and undulating behavior, where an adult eagle repetitively gains and loses altitude while simultaneously vocalizing (Watson 2010). Reproductive behavior included maintaining or incubating nests within the territory, which could be indicated by the presence of greenery in the nest. Nesting territories were also considered occupied if a pair was found to have produced offspring within the territory during subsequent surveys. Reproductive success was defined by at least one offspring fledging. Nesting territories that were found to be unoccupied were implicitly considered to have failed reproductively.

Supporting Variables

We accounted for variables known or strongly theorized to affect golden eagle reproductive success to more robustly estimate the effect and relative importance of proximity to target areas on reproductive success (Kochert et al. 1999; McGrady et al. 2002; Sergio et al. 2006; Watson 2010; Crandall et al. 2015; Lebeau et al. 2015; Wiens et al. 2018; Kochert et al. 2019). Variables included indices of disturbance, topography, prey habitat, intraspecific competition, weather, and water availability (Table 1). We derived all topographic indices from the 10 m digital elevation model, all vegetation indices from the LANDFIRE Existing Vegetation Type Layer 1.0.5 (LANDFIRE 2008, 2012 & 2014), and all weather indices from PRISM Climate Group (PRISM 2020) using ArcGIS Pro (ESRI 2018).

Indices included distance variables (e.g. distance to the nearest neighboring nest), home range variables (e.g. percent shrubland within the home range), and nest site variables (e.g. aspect). When nesting territories consisted of multiple nests, we used the centroid of nest sites within the territory to define the point of reference for distance variables. We defined home ranges as circular areas centered around each nest or nesting territory centroid (McIntyre et al. 2006; Watson et al. 2014). We estimated the average home range radius within the study area by dividing the average distance between neighboring nesting territories, excluding measures outside the 95% confidence interval, by two (Sergio et al. 2006). When home ranges overlapped, we bisected the area of overlap to divide the area equally between the two ranges (McGrady et al. 2002; Sergio et al. 2006). We used the average value across nest sites within a territory for nest site variables.

Target Area Effect Estimation

We estimated the effect of nesting territory proximity to target areas on Golden Eagle reproductive success using generalized linear mixed-effects models with a binomial response distribution. Yearly observations of nesting territory reproductive success comprised the observational units of the response. All models were constructed using R statistical software (R Core Team 2019).

We estimated the effect of nesting territory proximity to target areas while accounting for other variables known or theorized to affect Golden Eagle reproductive success by including them in a model selection process using the Akaike Information Criterion adjusted for small sample size (AICc) (Hurvich & Tsai 1989; Johnson & Omland 2004; Galipaud et al. 2017). Each candidate model represented an *a priori* competing hypothesis. Every candidate model included the null model parameters. Null model parameters consisted of the nesting territory proximity to target areas as the variable of interest (Grueber et al. 2011), in addition to 'nesting territory' and 'year' as random effects to account for lack of independence of yearly observations at the same territory (Gillies et al. 2006). We standardized all variables before model development to avoid issues with model convergence. We did not allow models to contain more than seven parameters (i.e. more than 1 parameter per 10 observations) to avoid overparameterization and overfit bias (Peduzzi et al., 1996). We did not allow models to contain highly correlated variables ($r \geq |0.6|$) to avoid collinearity. When variables were correlated, we added each variable to the null model and compared models using the AICc. We only included the variable in the model with the lowest AICc in subsequent analysis. We used the variance inflation factor (VIF) to test for multicollinearity among variables of all models. We discredited models with VIF > 10.

The number of models included in the model selection process regulates the tradeoff between the risk of failure to include models that might best approximate the underlying biological process, and the risk of spurious inclusion of meaningless models (Johnson & Omland 2004). We balanced this implicit tradeoff by organizing the model selection process using a two-stage, hierarchical framework (e.g. Carpenter et al. 2010; Baxter et al. 2017; Wiens et al. 2018). Following this framework, models are compared within discrete groups in the first stage and the best-performing model structures are advanced to the second stage. Thus, the first stage functions as an exploratory analysis that limits the number of total candidate models and regulates the implicit model selection tradeoff (Grueber et al. 2011).

In the first stage of model selection, we grouped variables based on the mechanism by which we hypothesized that the variable would affect reproductive success. Variables were grouped generally as either contributing to the exposure of the nest to predation and inclement weather or the foraging success of the parents (Table 1). When variables may have reasonably been hypothesized to affect reproductive success through either mechanism (e.g. nest site elevation may contribute to exposure or foraging success by affecting the energetic budget of the parents), we chose to include the variable in the group that seemed more biologically relevant (Crandall et al. 2015; Nielson et al. 2016). Models containing all combinations of variables up to six parameters were compared in each group. Competitive models (ΔAICc ≤ 2.0) were advanced to the next stage unless a model included uninformative parameters (Leroux 2019).

In the second stage of model selection we compared models that advanced from the first stage with models comprised of their combined structures. We also included models containing hypothesis-based interactions that were compatible with advancing model structures and the imposed limit of seven parameters. Although this process included a large number of candidate models (Supplemental Material), the risk of spurious model inclusion was mitigated by the hypothesis-based ecological justification of each model (Dochtermann & Jenkins 2010). The estimated effect of nesting territory proximity to target areas on Golden Eagle reproductive success was measured as the model-averaged variable coefficient of the competitive models (ΔAICc ≤ 2.0) resulting from the second stage of model selection.

Relative Variable Importance

We employed a balanced model selection approach to determine the relative effect of nesting territory proximity to target areas on reproductive success compared to other variables (Giam & Olden 2016). Following this approach, each variable, including the target area proximity variable, was included in the same number of models, and the null model included only the random effects. We maintained the two hypothesis-based groups of variables from the previous model selection process to reduce model collinearity. We tested all model combinations within each group up to five parameters to reduce the number of candidate models and the risk of spurious results. We estimated relative variable importance using the sum of model weights (SW) (Giam & Olden 2016) and the natural model average of each scaled coefficient (Galipaud et al. 2017).

RESULTS

Nesting Territory Surveys

There were 17 nesting territories within the study area, with an average spacing of 4.75 km, excluding outliers above the 95% confidence interval. The estimated home range radius was 2.38

km. On average, nesting territories were occupied in 85.0% of observations, but were reproductively successful in only 37.6% of observations. All nesting territories were occupied in at least one observation except the TTU territory, which was apparently abandoned and not surveyed after 2006 (Table 2). Reproductive success of nesting territories within target areas was polar. Of the five nesting territories established within target areas, three were reproductively successful in 0% of observations and two were reproductively successful in 100% of observations.

Target Area Effect Estimation

The distance to the nearest high-intensity target area, as defined *a priori* by biologists familiar with the UTTR, outperformed the distance to the nearest target area in preliminary analysis and was therefore used in all subsequent analyses. The best approximating model (w = 0.711), given the inclusion of the distance to the nearest high-intensity target area, consisted of the additive effects of the total precipitation of the previous year, the total precipitation during brood rearing, and the elevation of the nest site (Table 3; Supplemental Material). No other models were competitive (Table 3; Supplemental Material). Golden Eagles were not more likely to be reproductively successful in nesting territories that were farther away from high-intensity target areas ($\beta_{scaled} = 0.417 \pm 0.563$ se; $P = 0.460$; Fig. 2-2). However, Golden Eagles were more likely to be reproductively successful following years with higher total precipitation ($\beta_{scaled} = 1.622 \pm 0.628$ se; $P = 0.010$; Fig. 2-2) and in years with higher precipitation during brood rearing ($\beta_{scaled} = 1.729 \pm 0.759$ se; $P = 0.023$; Fig. 2-2). Golden Eagles were less likely to be reproductively successful in nesting territories at higher elevations ($\beta_{scaled} = -1.992 \pm 0.799$ se; $P = 0.013$; Fig. 2-2).

Relative Variable Importance

Of the seven uncorrelated variables that we hypothesized would affect Golden Eagle reproductive success by contributing to nest exposure, the distance to the nearest high-intensity target area variable ranked sixth and fifth in the sum of model weights (SW) and the natural model average of each scaled coefficient, respectively (Table 4). The most important exposure-related variables using these measures included nest site elevation, maximum mean temperature during brood rearing, and nest site terrain ruggedness index (Table 4). The least important exposure-related variables were the distance to the nearest road and the aspect (Table 4).

Of the eight uncorrelated variables that we hypothesized would affect Golden Eagle reproductive success by contributing to foraging success, the distance to the nearest high-intensity target area variable ranked seventh in both the SW and the natural model average of each scaled coefficient (Table 4). The most important foraging-related variables included total precipitation in the year prior to nesting, total precipitation during brood rearing, and percent of the home range dominated by shrubs (Table 4). The least important foraging-related variables, besides the distance to the nearest high-intensity target area, were home range topographic ruggedness index and total precipitation during nesting (Table 4).

DISCUSSION

Golden Eagles are a species of conservation concern in the western United States where threats including habitat loss, invasive species, and climate change may be contributing to population declines in some regions (Slater et al. 2013; Crandall et al. 2015; Tack et al. 2017). Adding to their conservation interest, Golden Eagles may be considered an umbrella species, as their conservation benefits a variety of species, particularly other obligate or facultative cliff-nesting birds such as Prairie Falcons, Ferruginous Hawks, Barn Owls, Great Horned Owls, and Common Ravens (Rodriguez et al. 2018). One potential threat to Golden Eagle populations in the western United States is repeated disturbance resulting from military tests and trainings (Schueck et al. 2001; Slater et al. 2013). Although unlikely to be directly harmful to Golden Eagles, explosive tests and trainings may elicit severe behavioral responses in nesting individuals, resulting in reduced reproductive success and local population instability (Schueck et al. 2001; Sih et al. 2011; Carlisle et al. 2018).

Given the best approximating model resulting from our selection process, which included variables for total precipitation in the year prior to nesting, total precipitation during brood rearing, and elevation of the nest site, we found that nesting territory proximity to sources of high-intensity explosive disturbance did not conclusively affect reproductive success. Furthermore, we found that nesting territory proximity to sources of high-intensity explosive disturbance consistently ranked below other habitat variables, such as nest site elevation and ruggedness, precipitation and temperature during brood rearing, and percent of the home range that was dominated by shrubs (Table 4).

The reproductive response of Golden Eagles to proximity to target areas appeared to be polar, with three of five nesting territories within target area boundaries exhibiting reproductive success in 0% of observations, and the remaining two nesting territories exhibiting reproductive success in 100% of observations (Table 2). This duality may indicate an interaction between disturbance and some other habitat or behavioral component that we failed to detect. For example, the effect of the disturbance on reproductive success may have depended on the experience or fitness of the eagles occupying the territory (Slater et al. 2013). Of the nesting territories situated within target area boundaries, the TTU nesting territory is of particular conservation interest as it was the only territory to apparently have been abandoned (Calrisle et al. 2018; Table 2). The TTU territory is situated within the boundaries of an exceptionally high-intensity target area and is characterized by the lowest percentage of shrubland within the home range of all of the observed nesting territories. This territory may have been abandoned as a result of severe disturbance or reduced shrubland and cheatgrass invasion that resulted from fires associated with explosive testing (Kochert & Steenhof 2012; Slater et al. 2013; Lindenmayer et al. 2016; Spaul & Heath 2016). Alternatively, the TTU territory may have been abandoned for reasons unrelated to the suitability of the habitat, such as the death of the pair that had been occupying the territory (Kochert & Steenhof 2012).

Failure to identify an association between explosive disturbance and Golden Eagle reproductive success may have been a result of limitations typical of observational studies rather than true ecological processes. For example, model selection is not sensitive to rare events that have large effects (Burnham & Anderson 2002). Thus, our methods may have resulted in a Type II error if explosive disturbance did have a strong effect on reproductive success, but in only a few observations, as may have been the case with the TTU territory (Table 2). Furthermore, many of the variables included in the model selection process were characterized by low precision or accuracy. For example, because nesting territories were the observational unit rather than individual nests, nest site variables such as elevation and aspect were averaged across all the nests in the territory, which likely did not reflect the actual conditions of the occupied nest. The nesting territory proximity to target areas was also characterized by low precision due to expected military constraints (Hanson 2018). The combined imprecision of these variables precluded inclusion of the line of sight from the nest to sources of disturbance as an explanatory variable, although visual exposure to the disturbance may have a strong effect on the behavioral responses of nesting eagles (Camp et al. 1997). Other variables associated with the source of disturbance that may have influenced the responses of nesting eagles, such as the timing, frequency, and severity of the disturbance, were also precluded my military constraints (Rankin et al. 2009). As the patterns of disturbance are known to affect behavioral responses, the proximity to sources of explosive disturbance may ultimately have been a poor measure of the disturbance (Rankin et al. 2009; Crandall et al. 2015).

The reproductive response of Golden Eagles to explosive disturbance may have been mitigated through behavior (Rankin et al. 2009; Grubb et al. 2010; Sih et al. 2011). For example, Golden Eagles may have mitigated the reproductive response through habitat selection, by constructing or using nests farther away from, or topographically shielded from, sources of explosive disturbance (Grubb et al. 2010). As a non-exclusionary alternative, Golden Eagles may have habituated to explosive disturbance over time. As an intelligent, long-lived species exhibiting high nesting territory fidelity and behavioral plasticity, the potential for Golden Eagles to habituate to disturbances that frequently occur in close proximity to their territories is high (Kochert et al. 2002; Rankin et al. 2009; Sih et al. 2011; Preston et al. 2017). However, according to predominant habituation theory, Golden Eagles would be less likely to habituate to explosive disturbance if it was infrequent, intense, or diverse (Rankin et al. 2009). Furthermore, Golden Eagles newly exposed to disturbance, either by appropriating a territory in proximity to a target area, or by the construction of a target area in close proximity to an existing nesting territory, would likely respond increasingly severely initially (i.e. within the first one or more breeding attempts) followed by a decrementing response over time (Rankin et al. 2009).

The time-intensive and fickle process of habituation to novel disturbances highlights the importance of maintaining disturbances within designated areas where they are least likely to have a strong impact on species of conservation concern (Rankin et al. 2009; Zentelis et al. 2017). On the UTTR and similar ranges, Golden Eagle conservation may be promoted by isolating tests and trainings to areas far from cliffs that provide nesting habitat (Slater et al. 2013; Spaul & Heath 2016). Tests and trainings should be especially isolated from existing nesting territories that are consistently reproductively successful and may be susceptible to novel disturbances (Slater et al. 2013; Wiens et al. 2018).

The reproductive success and conservation of Golden Eagles within the UTTR and similar areas may also be promoted by addressing the habitat components that were shown to have significant effects and high relative importance (Fig. 2-1; Table 4). The significance and high relative importance of variables associated with precipitation and shrub cover suggests that reproductive success was affected by bottom-up processes mediating jackrabbit densities (Kelt 2011; Simes et al. 2015; Wiens et al. 2018). Thus, management focused on restoring shrub cover may improve Golden Eagle reproductive success within the study area (Kochert et al. 1999; Slater et al. 2013). Topographic and weather variables related to exposure were also relatively important and may be mitigated by installing structures that provide cover over nests (Allsion et al. 2017; Kochert et al. 2019; Table 4). These management strategies would also serve to mitigate any potentially negative effects of military tests and trainings on Golden Eagle reproductive success and population stability (Allsion et al. 2017; Kochert et al. 2019).

In conclusion, we found no definitive evidence of an effect of explosive disturbance related to military tests and trainings on Golden Eagle reproductive success. This may have been a result of failure of explanatory variables to reflect the true conditions affecting Golden Eagle biology and behavior. Alternatively, Golden Eagles may have behaviorally mediated their response to disturbance through processes of habitat selection or habituation. In order to more conclusively estimate the potential effect of explosive disturbance on Golden Eagle reproductive success, future research would need to record stimulus sound simultaneously with behavioral response and subsequent nest success, perhaps using sound monitors and remote cameras (Grubb et al. 2010). In the absence of such data, we recommend continuing to isolate military tests and trainings from Golden Eagle nesting habitat, and especially highly productive nesting territories in the UTTR and similar areas. As Golden Eagles in the western United States face the threats of habitat loss associated with climate change and invasive species, military areas such as the UTTR, under careful management, could play a key role in promoting Golden Eagle conservation (Slater et al. 2013; Crandall et al. 2015; Zentelis et al. 2017).

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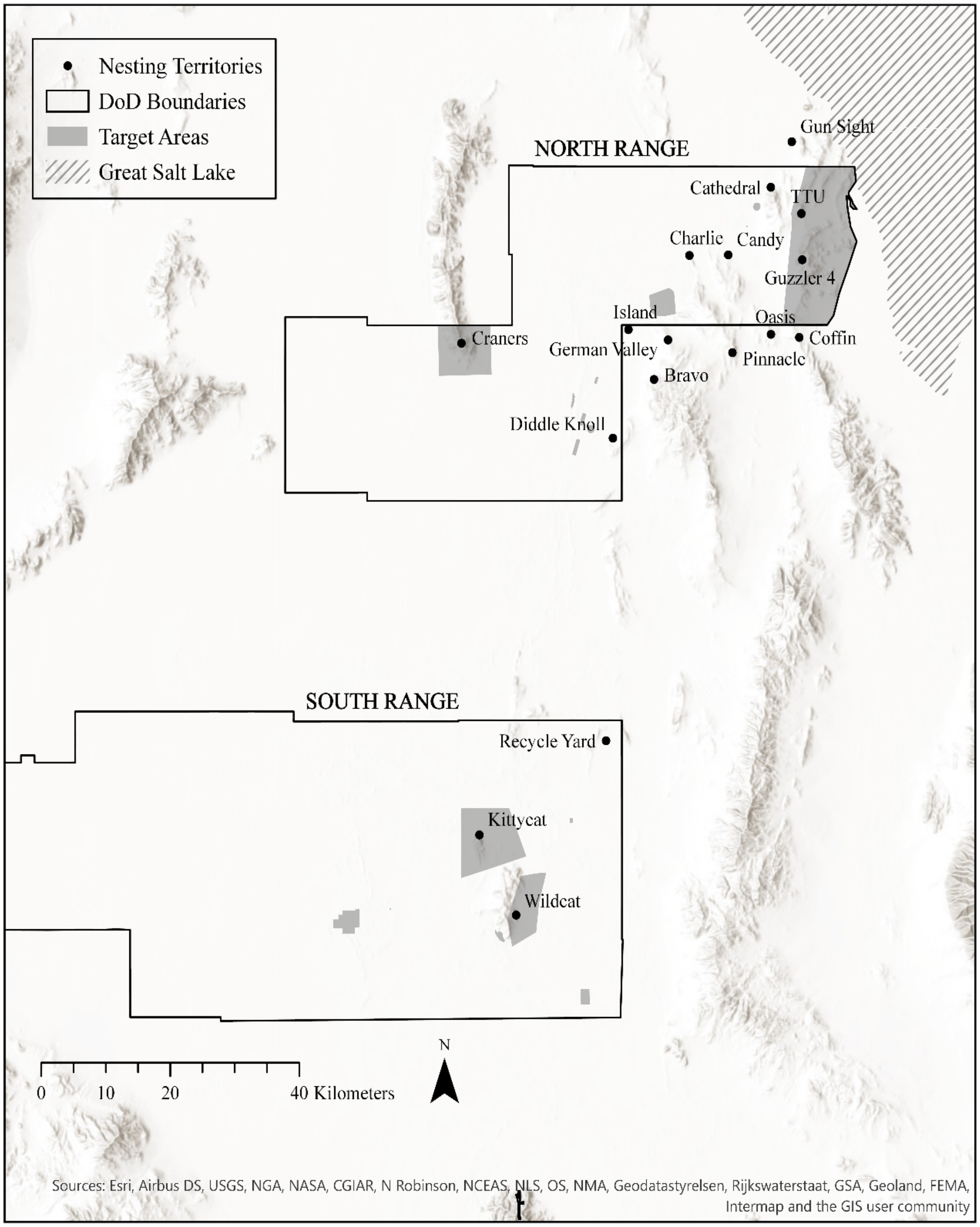
FIGURES



Sources: Esri, Airbus DS, USGS, NGA, NASA, CGIAR, N Robinson, NCEAS, NLS, OS, NMA, Geodatastyrelsen, Rijkswaterstaat, GSA, Geoland, FEMA, Intermap and the GIS user community

Figure 2-1. A map of the known Golden Eagle nesting territories within and surrounding the Utah Test and Training Range. Explosive target areas are also depicted. Although some nesting territories exist within designated target areas, nest sites are strictly protected from direct harm.

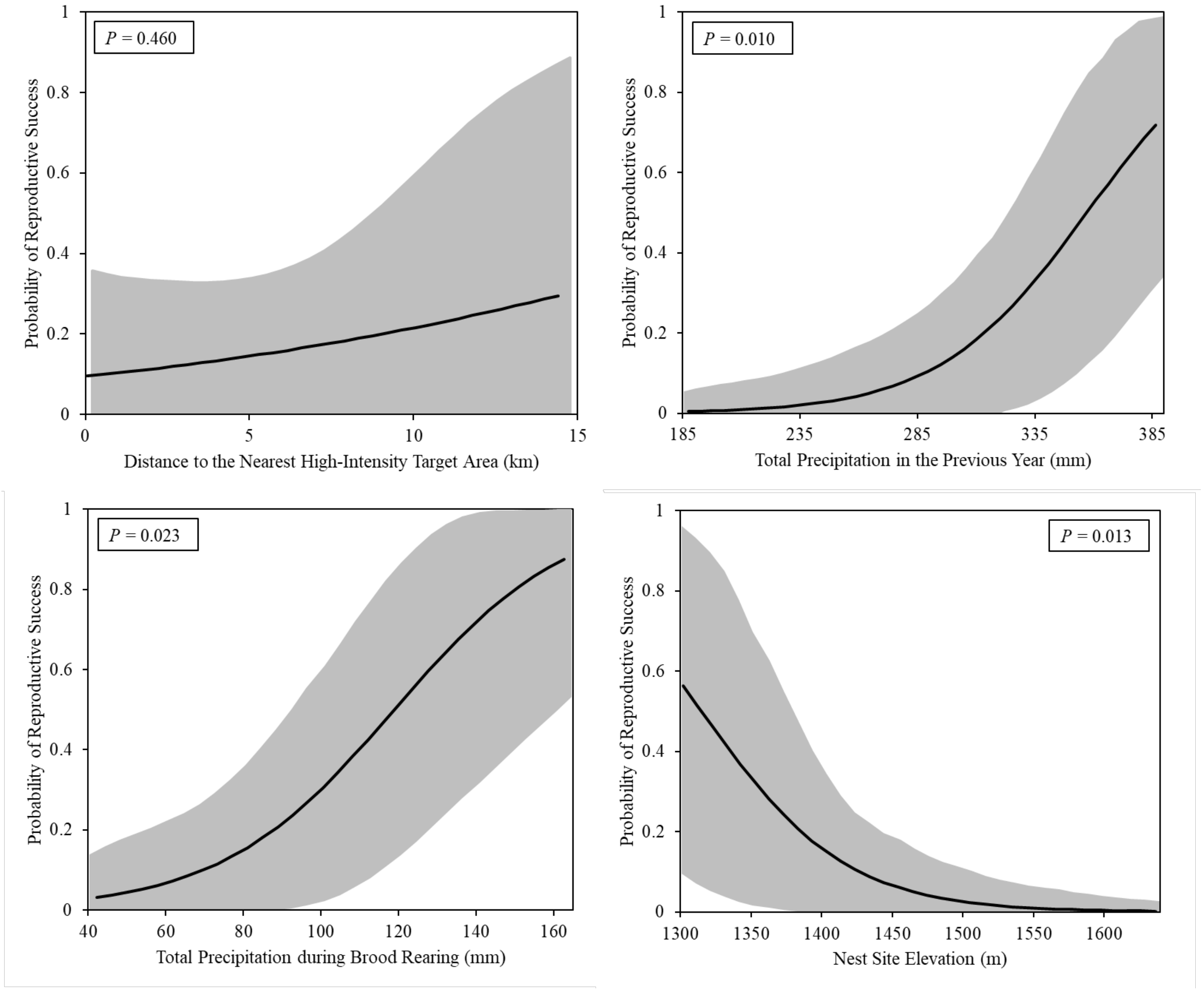


Figure 2-2. Estimated probabilities of reproductive success in response to each explanatory variable in the best approximating model, holding the remaining variables constant at their respective median values. In each case, the range of the explanatory variable reflects the actual range of the data to avoid extrapolation. The shaded areas represent bootstrapped 95% prediction intervals.

TABLES

Table 2-1. A list of variables known or theorized to affect Golden Eagle reproductive success that were included in the model selection process (Kochert et al. 1999; McGrady et al. 2002; Sergio et al. 2006; Watson 2010; Crandall et al. 2015; Lebeau et al. 2015; Wiens et al. 2018; Kochert et al. 2019).

Variables Hypothesized to Affect Reproductive Success by Contributing to Nest Exposure	
Variable Description	Abbreviation
Distance to the nearest target area	TA
Square of the distance to the nearest target area for nonlinear effects	TA2
Distance to the nearest high-intensity target area	TAH
Square of the distance to the nearest high-intensity target area for nonlinear effects	TAH2
Mean terrain ruggedness index value at the nest site	NS_TRI
Square of the mean terrain ruggedness index value at the nest site for nonlinear effects	NS_TRI2
Mean topographic position index value at the nest site	NS_TPI
Square of the mean topographic position index value at the nest site for nonlinear effects	NS_TPI2
Cosine of the aspect of the nest site measured in degrees (i.e. the northness)	ASPECT
Slope of the nest site (%)	SLOPE
Square of the slope of the nest site (%)	SLOPE2
Elevation of the nest site (m)	ELEV
Square of elevation for nonlinear effects	ELEV2
Maximum mean temperature during brood rearing (April - June; °C)	MMT
Distance to the nearest road (m)	ROAD
Squared distance to the nearest road for non-linear effects	ROAD2

Variables Hypothesized to Affect Reproductive Success by Contributing to Foraging Success	
Variable Description	Abbreviation
Mean terrain ruggedness index value within the home range	HR_TRI
Mean topographic position index value within the home range	HR_TPI
Percent of the home range classified as shrubland	SHRUB
Simpson's diversity index of vegetation classes within the home range	SIMPS
Distance to the nearest water source (m)	WATER
Squared distance to the nearest water source for non-linear effects	WATER2
Distance to the nearest conspecific nesting territory (m)	NND
Squared distance to the nearest conspecific nesting territory for non-linear effects	NND2
Total precipitation in the previous year (mm)	PPY
Total precipitation during early nesting (December - March; mm)	PNEST
Total precipitation during brood rearing (April - June; mm)	PBROOD

Table 2-2. A summary of nesting territory occupancy and reproductive success in relation to proximity to target areas. Territories were surveyed in 2006, 2012, 2013, and 2015-2018. Of note, the TTU territory was only surveyed in 2006 as it appeared to have been abandoned. Although some nesting territories exist within designated target areas, nest sites are strictly protected from direct harm.

Nesting Territory	Distance to Target Area (m)	Average Occupancy (%)	Average Reproductive Success (%)	$N_{\text{Reproductive Success}}$
Craners	0	100.0	100.0	4
Guzzler 4	0	85.7	0.0	7
Kittycat	0	100.0	0.0	2
TTU	0	0.0	0.0	1
Wildcat	0	100.0	100.0	4
Coffin	1464	60.0	0.0	5
Oasis	1812	100.0	0.0	5
Cathedral	2176	100.0	71.4	7
Diddle Knoll	2347	100.0	66.7	6
German Valley	2637	66.7	20.0	5
Gun Sight	3254	100.0	40.0	5
Island	3303	83.3	33.3	6
Candy	3759	100.0	66.7	6
Charlie	4225	100.0	66.7	6
Pinnacle	5539	50.0	0.0	4
Bravo	6451	100.0	50.0	2
Recycle Yard	6946	100.0	25.0	4
	Average	85.0	37.6	

Table 2-3. A summary of the competitive models within the hypothesis-based 2-stage hierarchical model selection process detailing the model structures, number of parameters (K), Akaike's Information Criterion corrected for small sample size (AICc), the log likelihood (LL), the change in AICc (ΔAICc), and the model weight (ωi). The territory (TERR) and year (YEAR) were included in all models as random effects.

Stage 1

Group 1: Variables Hypothesized to Affect Reproductive Success by Contributing to Nest Exposure

Model Structure	*K*	AIC_c	LL	ΔAIC_c	ω_i
TERR + YEAR + TAH + ELEV	5	-41.31	93.43	0.00	0.13
TERR + YEAR + TAH + NS_TRI + MMT	6	-40.48	94.14	0.70	0.09
TERR + YEAR + TAH + MMT	5	-41.72	94.26	0.83	0.09

Group 2: Variables Hypothesized to Affect Reproductive Success by Contributing to Foraging Success

Model Structure	*K*	AIC_c	LL	ΔAIC_c	ω_i
TERR + YEAR + TAH + PPY + PBROOD	6	-37.16	87.48	0.00	0.38
TERR + YEAR + TAH + SIMPS + PBROOD	6	-37.78	88.73	1.25	0.20

Stage 2

Model Structure	*K*	AIC_c	LL	ΔAIC_c	ω_i
TERR + YEAR +TAH + ELEV + PBROOD + PPY	7	-32.91	81.39	0.00	0.71

Table 2-4. The relative importance of habitat variables as measured by the sum of model weights (SW) and the scaled variable coefficient (β).

Group 1: Variables Hypothesized to Affect Reproductive Success by Contributing to Nest Exposure				
Rank	Variable	SW	Variable	β
1	ELEV	0.534	ELEV	-1.86
2	MMT	0.404	NS_TRI	1.20
3	NS_TRI	0.293	MMT	1.20
4	NS_TPI	0.131	NS_TPI	-0.61
5	ROAD	0.115	TAH	0.33
6	TAH	0.103	ASPECT	0.27
7	ASPECT	0.097	ROAD	-0.24

Group 2: Variables Hypothesized to Affect Reproductive Success by Contributing to Foraging Success				
Rank	Variable	SW	Variable	β
1	PBROOD	0.757	PBROOD	1.80
2	PPY	0.410	SHRUB	1.59
3	SIMPS	0.195	NND	1.47
4	NND	0.161	SIMPS	-1.40
5	SHRUB	0.158	PPY	1.25
6	PNEST	0.092	PNEST	1.19
7	TAH	0.062	TAH	0.80
8	HR_TRI	0.041	HR_TRI	0.40

SUPPLEMENTAL MATERIAL

Table S1**.** A complete summary of the hypothesis-based 2-stage hierarchical model selection process including the model structures, number of parameters (K), Akaike's Information Criterion corrected for small sample size (AICc), the log likelihood (LL), the change in AICc (ΔAICc), and the model weight (ωi). The territory (TERR) and year (YEAR) were included in all models as random effects.

Stage 1

Group 1: Variables Hypothesized to Affect Reproductive Success by Contributing to Nest Exposure

Model Structure	K	AIC_c	LL	ΔAIC_c	ω_i
TERR + YEAR + TAH + ELEV	5	-41.31	93.43	0.00	0.13
TERR + YEAR + TAH + ELEV + MMT	6	-40.16	93.49	0.05	0.13
TERR + YEAR + TAH + NS_TRI + ELEV	6	-40.30	93.76	0.33	0.11
TERR + YEAR + TAH + NS_TRI + MMT	6	-40.48	94.14	0.70	0.09
TERR + YEAR + TAH + MMT	5	-41.72	94.26	0.83	0.09
TERR + YEAR + TAH + NS_TPI + ELEV	6	-41.15	95.46	2.03	0.05
TERR + YEAR + TAH + NS_TRI	5	-42.33	95.47	2.04	0.05
TERR + YEAR + TAH + ASPECT + ELEV	6	-41.26	95.69	2.26	0.04
TERR + YEAR + TAH + ROAD + ELEV	6	-41.30	95.77	2.33	0.04
TERR + YEAR + TAH + NS_TPI + MMT	6	-41.31	95.78	2.35	0.04
TERR + YEAR + TAH + ROAD + MMT	6	-41.48	96.12	2.69	0.03
TERR + YEAR + TAH + NS_TRI + NS_TPI	6	-41.49	96.14	2.71	0.03
TERR + YEAR + TAH	4	-43.88	96.31	2.87	0.03
TERR + YEAR + TAH + ROAD + NS_TRI	6	-41.63	96.42	2.98	0.03
TERR + YEAR + TAH + ASPECT + MMT	6	-41.72	96.60	3.16	0.03
TERR + YEAR + TAH + NS_TRI + ASPECT	6	-42.31	97.79	4.35	0.02
TERR + YEAR + TAH + ROAD	5	-43.52	97.86	4.43	0.01
TERR + YEAR + TAH + NS_TPI	5	-43.65	98.13	4.70	0.01
TERR + YEAR + TAH + ASPECT	5	-43.87	98.56	5.13	0.01
TERR + YEAR + TAH + ROAD + NS_TPI	6	-43.46	100.10	6.66	0.00
TERR + YEAR + TAH + ROAD + ASPECT	6	-43.52	100.20	6.77	0.00
TERR + YEAR + TAH + NS_TPI + ASPECT	6	-43.64	100.45	7.01	0.00

Group 2: Variables Hypothesized to Affect Reproductive Success by Contributing to Foraging Success

Model Structure	K	AIC_c	LL	ΔAIC_c	ω_i
TERR + YEAR + TAH + PPY + PBROOD	6	-37.16	87.48	0.00	0.38
TERR + YEAR + TAH + SIMPS + PBROOD	6	-37.78	88.73	1.25	0.20
TERR + YEAR + TAH + SIMPS + NND	6	-38.65	90.47	2.99	0.09
TERR + YEAR + TAH + PBROOD + PNEST	6	-39.28	91.72	4.24	0.05
TERR + YEAR + TAH + SIMPS + PPY	6	-39.48	92.12	4.64	0.04
TERR + YEAR + TAH + SHRUB + PBROOD	6	-39.54	92.24	4.76	0.04

TERR + YEAR + TAH + PBROOD	5	-40.79	92.39	4.91	0.03
TERR + YEAR + TAH + NND + PBROOD	6	-39.63	92.43	4.95	0.03
TERR + YEAR + TAH + SIMPS	5	-40.95	92.72	5.24	0.03
TERR + YEAR + TAH + SHRUB + SIMPS	6	-39.95	93.07	5.59	0.02
TERR + YEAR + TAH + SIMPS + PNEST	6	-40.43	94.02	6.54	0.01
TERR + YEAR + TAH + HR_TRI + PBROOD	6	-40.51	94.18	6.70	0.01
TERR + YEAR + TAH + SIMPS + HR_TRI	6	-40.67	94.52	7.04	0.01
TERR + YEAR + TAH + SHRUB + PPY	6	-41.31	95.79	8.31	0.01
TERR + YEAR + TAH + SHRUB	5	-42.49	95.80	8.32	0.01
TERR + YEAR + TAH + PPY	5	-42.49	95.80	8.32	0.01
TERR + YEAR + TAH + NND	5	-42.64	96.10	8.62	0.01
TERR + YEAR + TAH + SHRUB + NND	6	-41.53	96.24	8.75	0.00
TERR + YEAR + TAH	4	-43.88	96.31	8.83	0.00
TERR + YEAR + TAH + NND + PPY	6	-41.85	96.86	9.38	0.00
TERR + YEAR + TAH + SHRUB + PNEST	6	-42.13	97.42	9.94	0.00
TERR + YEAR + TAH + PNEST	5	-43.43	97.69	10.21	0.00
TERR + YEAR + TAH + HR_TRI	5	-43.47	97.76	10.28	0.00
TERR + YEAR + TAH + SHRUB + HR_TRI	6	-42.31	97.79	10.31	0.00
TERR + YEAR + TAH + HR_TRI + PPY	6	-42.35	97.87	10.39	0.00
TERR + YEAR + TAH + NND + PNEST	6	-42.37	97.90	10.42	0.00
TERR + YEAR + TAH + PPY + PNEST	6	-42.48	98.13	10.64	0.00
TERR + YEAR + TAH + HR_TRI + NND	6	-42.58	98.33	10.85	0.00
TERR + YEAR + TAH + HR_TRI + PNEST	6	-43.13	99.42	11.94	0.00

Stage 2					
Model Structure	K	AIC_c	LL	ΔAIC_c	ω_i
TERR + YEAR +TAH + ELEV + PBROOD + PPY	7	-32.91	81.39	0.00	0.71
TERR + YEAR * TAH + PBROOD + PPY	6	-37.16	87.48	6.09	0.03
TERR + YEAR +TAH + PBROOD + PPY	6	-37.16	87.48	6.09	0.03
YEAR + TERR * TAH + PBROOD + PPY	6	-37.16	87.48	6.09	0.03
TERR + YEAR +TAH+ SIMPS * PBROOD	7	-36.06	87.70	6.31	0.03
TERR + YEAR +TAH + ELEV + PBROOD + SIMPS	7	-36.09	87.76	6.37	0.03
TERR + YEAR +TAH + PBROOD + SIMPS	6	-37.78	88.73	7.34	0.02
YEAR + TERR * TAH + PBROOD + SIMPS	6	-37.78	88.73	7.34	0.02
TERR + YEAR + TAH + PPY * PBROOD	7	-36.77	89.12	7.73	0.01
TERR + YEAR + TAH * PBROOD + PPY	7	-37.03	89.64	8.25	0.01
TERR + YEAR + TAH + MMT + PBROOD + PPY	7	-37.06	89.70	8.31	0.01
TERR + YEAR + TAH * PPY + PBROOD	7	-37.14	89.86	8.47	0.01
TERR + YEAR + TAH + MMT + PBROOD + SIMPS	7	-37.22	90.01	8.62	0.01
TERR + YEAR + TAH * SIMPS + PBROOD	7	-37.73	91.05	9.66	0.01
TERR + YEAR + TAH * PBROOD + SIMPS	7	-37.75	91.07	9.68	0.01

TERR + YEAR * TAH + PBROOD + SIMPS	6	-39.11	91.39	10.00	0.00
TERR + YEAR + TAH + ELEV * MMT	7	-37.99	91.56	10.17	0.00
TERR + YEAR + TAH + ELEV	5	-41.31	93.43	12.04	0.00
YEAR + TERR * TAH + ELEV	5	-41.31	93.43	12.04	0.00
TERR + YEAR + TAH + MMT + NS_TRI	6	-40.48	94.14	12.75	0.00
YEAR + TERR * TAH + MMT + NS_TRI	6	-40.48	94.14	12.75	0.00
TERR + YEAR + TAH + MMT	5	-41.72	94.26	12.87	0.00
YEAR + TERR * TAH + MMT	5	-41.72	94.26	12.87	0.00
TERR + YEAR + TAH + ELEV + MMT + NS_TRI	7	-39.37	94.33	12.94	0.00
TERR + YEAR + TAH * ELEV	6	-41.21	95.59	14.20	0.00
TERR + YEAR + TAH * ELEV + MMT	7	-40.13	95.85	14.46	0.00
TERR + YEAR + TAH * MMT + ELEV	7	-40.16	95.89	14.50	0.00
TERR + YEAR + TAH + NS_TRI * MMT	7	-40.22	96.01	14.62	0.00
TERR + YEAR * TAH + MMT + NS_TRI	6	-41.53	96.22	14.83	0.00
TERR + YEAR * TAH + MMT	5	-42.73	96.29	14.90	0.00
TERR + YEAR + TAH * MMT + NS_TRI	7	-40.46	96.50	15.11	0.00
TERR + YEAR + TAH * NS_TRI + MMT	7	-40.48	96.55	15.16	0.00
TERR + YEAR + TAH * MMT	6	-41.71	96.58	15.19	0.00
TERR + YEAR * TAH + ELEV	5	-45.46	101.74	20.35	0.00