



Research Article

Wind Energy, Nest Success, and Post-Fledging Survival of *Buteo* Hawks

PATRICK S. KOLAR,¹ Raptor Research Center, Department of Biological Science, Boise State University, 1910 University Drive, Boise, ID 83725, USA

MARC J. BECHARD, Raptor Research Center, Department of Biological Science, Boise State University, 1910 University Drive, Boise, ID 83725, USA

ABSTRACT Quantifying the rate of turbine collision mortality for raptors has been the primary focus of research at wind energy projects in Europe and the United States. Breeding adults and fledglings may be especially prone to collisions, but few studies have assessed the consequences of increased mortality and indirect effects from this type of development activity on reproduction. We examined the influence of wind turbines and other factors on nest success and survival of radio-marked juveniles during the post-fledging period for 3 sympatric breeding *Buteo* species in the Columbia Plateau Ecoregion (CPE), Oregon, USA. Nest success for ferruginous hawks (*Buteo regalis*) decreased as the number of wind turbines within the home range buffer (32 km²) increased. There was no effect of turbines on nest success for red-tailed hawks (*Buteo jamaicensis*) or Swainson's hawks (*Buteo swainsoni*). Of 60 nestlings radio-marked from all 3 species, we found no evidence that any were killed as a result of collisions with wind turbines after fledging. This was likely due, in part, to the limited size of the natal home range and the relatively short duration of the post-fledging period. However, juveniles of all 3 species hatched from nests in areas of greater turbine density were more likely to die from predation or starvation just after fledging and prior to becoming independent compared to those in areas of lower turbine density. Taken together, these results suggest that wind turbines affected reproductive efforts by all 3 species to some degree, but these effects were greater for ferruginous hawks compared to the other 2 congeneric species. The causes of this negative association are unknown but likely represent some combination of breeding adults being killed from turbine collisions, disturbed from activities associated with the increasing wind energy development in the area, or displaced from portions of their home range to minimize the risk of disturbance or death. The potential for these effects necessitate that planning of future wind energy facilities be considered at larger geographic scales beyond the placement of individual turbines to limit development near raptor breeding areas. © 2016 The Wildlife Society.

KEY WORDS *Buteo* hawk, ferruginous hawk, juvenile survival, nest success, nest survival, post-fledging period, red-tailed hawk, Swainson's hawk, wind energy, wind turbines.

Production of energy through wind power has rapidly expanded during recent years as local and regional governments worldwide set ambitious mandates for wind and other sources of renewable energy. Wind energy generation is considered an essential component to combat global climate change because it does not produce polluting emissions (e.g., carbon dioxide). Yet, even as wildlife managers begin to grapple with the effects of increasing temperatures on wildlife populations (Mawdsley et al. 2009), they are tasked with balancing the need for increased production of renewable energy with the risk of some adverse effects to wildlife resulting from these developments. Impacts to wildlife from wind energy development (e.g., collisions with

turbines, habitat loss, disturbance, and displacement from foraging or nesting areas) have been documented for many species (Drewitt and Langston 2006, Madders and Whitfield 2006, Marques et al. 2014, May 2015). In some cases, infrastructure associated with energy development may benefit raptors and offset these impacts, including increased prey densities along edge habitat associated with access roads (Schmutz 1989, Zelenak and Rotella 1997, Keough and Conover 2012) and structures such as transmission towers and power line poles used for perching and nesting (Benítez-López et al. 2010). Road development has also been linked to increased illegal raptor shooting (Lehman et al. 2010) and vehicle collisions. Raptors perching on older-generation wind turbines with lattice towers and developments constructed in areas with high densities of prey are considered the 2 factors contributing to increased collision rates in some areas (Osborn et al. 1998, Smallwood et al. 2009). Any such impacts are of particular concern for raptors

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¹E-mail: pskolar@yahoo.com

because they are generally long-lived and have low reproductive rates. As a result, even small impacts that reduce survival might affect population growth rates (Sæther and Bakke 2000, Carrete et al. 2009).

Quantifying the rate of turbine collision mortality for raptors after construction has been the primary focus of research in Europe and the United States, but estimates may not account for other indirect factors that might contribute to population-level effects of wind energy development. The disturbance-risk hypothesis (Frid and Dill 2002) provides a theoretical framework to explain, in part, the response of animals to non-lethal stimuli resulting from anthropogenic activities that induce a response similar to antipredator behavior and can indirectly reduce survival and reproduction. Disturbances may cause animals to be pushed into suboptimal habitats or areas with greater intraspecific competition, or increase energy expenditure that can compromise fitness and contribute to higher predation rates (May 2015). Breeding raptors exposed to other types of anthropogenic activity alter their spatial use of the landscape and make extra-home range movements (Andersen et al. 1990), or abandon nests altogether (White and Thurow 1985). Many studies have reported that displacement and disturbance effects from wind energy development occurring at a variety of spatial scales, from vacancy of nesting areas to changes in movement patterns and turbine avoidance within the home range, are negligible (Madders and Whitfield 2006, Hernández-Pliego et al. 2015) or inconclusive for some raptors (Drewitt and Langston 2006); however, other studies report they suspected displacement by wind energy development as the primary reason for decreased abundance (Farfán et al. 2009, Pearce-Higgins et al. 2009, Garvin et al. 2011, Dahl et al. 2012). These inconsistencies likely vary depending upon the extent of development and species-specific tolerance to disturbance (May 2015). Thus, these indirect effects may be a greater concern for uncommon raptors (e.g., state or federally listed species) and those that are more sensitive to disturbance and less likely to be found as collision fatalities.

The risk of collisions may also depend upon age- and stage-specific mortality and examining survival at all stages in life is necessary to accurately determine the cumulative effects of wind energy development on population growth (Carrete et al. 2009). The post-fledging dependency period, an important component of reproduction, is one such important life-history stage that is rarely studied (Steenhof and Newton 2007) but may be affected by wind energy development. Survival of young during this developmental period is still contingent upon protection and provisioning from adults (Bechard and Schmutz 1995, McClaren et al. 2005, Preston and Beane 2009, Bechard et al. 2010), but fledglings and territorial pairs may also be more susceptible to collision with turbines if located close to their breeding areas (Carrete et al. 2009). Further, fledglings gradually increase the intensity of activity within the natal range and may have limited ability to avoid turbines while flight skills are still developing. Many fatalities of juveniles at some wind energy facilities occur during the post-fledging period (Barrios and Rodriguez

2004), suggesting this age class may be disproportionately affected.

We used 3 *Buteo* hawk species that vary in their tolerance to anthropogenic activity as model organisms to address some of the global knowledge gaps regarding impacts of wind energy development on reproduction. Of these, ferruginous hawks (*Buteo regalis*) are reported to be particularly sensitive to human disturbance during the nesting season in some cases (White and Thurow 1985, Keeley and Bechard 2011) and are listed as Sensitive-critical in Oregon and Threatened in Washington (Washington Department of Fish and Wildlife 1996) within their range in the Columbia Plateau Ecoregion (CPE; Thorson et al. 2003). The Oregon Conservation Strategy lists impacts from wind turbines in the Columbia Plateau as a data gap for this species (Oregon Department of Fish and Wildlife 2006). The 2 sympatric *Buteo* species, Swainson's hawks (*Buteo swainsoni*) and red-tailed hawks (*Buteo jamaicensis*), are seemingly tolerant of human activity (Preston and Beane 2009, Bechard et al. 2010).

Given the potential for collision mortality of adults and fledglings, but with differing responses of these *Buteo* species to anthropogenic disturbance, our objective was to determine if wind energy development affected nest success and post-fledging survival. We also wanted to account for the effect of other natural sources of variation that are important to these species. We predicted that reproductive measures would be negatively affected by wind turbines if breeding *Buteo* pairs were directly or indirectly affected, especially ferruginous hawks. Additionally, we predicted that decreased proximity to intra- and inter-specific breeding pairs would negatively affect nest success and post-fledging survival for these 3 congeneric species (Schmutz et al. 1980, Zelenak and Rotella 1997). Nesting ferruginous hawks are often associated with high percentages of grassland vegetation and low percentages of cultivated wheat (Schmutz 1989, Zelenak and Rotella 1997) compared to red-tailed hawks and Swainson's hawks (Schmutz 1989, Bechard et al. 1990). Thus, we predicted a similar relationship between vegetation types and reproduction in our study as that found in their sympatric ranges elsewhere in the western United States. Previous studies have shown nesting chronology (Steenhof et al. 1997), reproduction (Steenhof and Kochert 1985), and nestling survival (Bechard 1983) of *Buteo* hawks to vary annually and seasonally in response to fluctuations of dominant prey types. Survival may also vary during the post-fledging period because juvenile raptors are more susceptible to mortality initially after leaving the nest, when they are relatively sedentary but not able to avoid predators, and just prior to reaching independence when starvation is a common source of death (Watson 2003, Wiens et al. 2006). Therefore, we also predicted similar natural temporal fluctuations in these reproductive parameters with survival being highest during the middle and later stages of nesting and the post-fledging period. Our specific objectives were to determine what landscape-scale and nest variables best explain variation in nest success, examine sources of mortality for fledglings and determine the influence of variables on post-fledging

survival, and determine whether the timing of nest initiation would indicate a preferential selection of nesting areas in relation to wind turbine variables.

STUDY AREA

The 504-km² study area was located in Gilliam and Morrow counties near Arlington, Oregon (Fig. 1). This area is considered a lowland high desert with a semi-arid climate consisting of cool winters and hot summers. Elevation of the high plateaus, rolling hills, and steep basalt canyons within the study area ranged from 85 m along the Columbia River, delineating the northern boundary, to 420 m above sea level. Land cover and vegetation types within the study area occurred as a mosaic that was consistent throughout the CPE (Oregon Department of Fish and Wildlife 2006) including shrub-steppe, grasslands, dryland wheat, and irrigated croplands. However, most of the non-agricultural vegetation consisted of introduced grasses with remnant patches of sagebrush (*Artemisia* spp.) and rabbitbrush (*Chrysothamnus* spp.) shrubs. Much of the land in the study area was privately owned and used for agriculture and livestock grazing. Additional land use activities included development for industrial transport and waste storage associated with the Columbia Ridge Landfill, small gravel quarry operations, and construction of future wind projects and associated infrastructure (e.g., access roads, transmission lines, operations and maintenance buildings, electrical substations).

The study area included 7 total wind energy projects, 5 of which contained 257 wind turbines that were constructed and became operational from 2006–2009. One additional

wind project was under construction in 2010 and became operational with 117 wind turbines in early 2011. The study area also included one wind energy project in the permitting phase of development and areas that were not related to wind energy development (The Nature Conservancy's Boardman Conservation Area, Bureau of Land Management land, and privately owned land). Most of the 374 turbines in the developed project areas were arranged in strings of 2 to 18 turbines, running north-south along ridges and plateaus, and spaced approximately 100–260 m apart within each string. The wind turbines were all newer-generation 2.1-megawatt Suzlon S88 (Suzlon, Magarpatta City, India) turbines with a rotor diameter of 88 m and tower height of 79 m, or 1.5-megawatt General Electric SLE (General Electric, Fairfield, Connecticut, USA) turbines with a rotor diameter of 77 m and tower height of 80 m, both with tubular towers.

METHODS

Study Design and Radio-Marking

In 2010 and 2011, we searched all historical and potentially suitable nesting substrates for each species of *Buteo* hawks (Bechard and Schmutz 1995, Preston and Beane 2009, Bechard et al. 2010) with ground surveys up to 5.5 km from the nearest wind turbine (Fig. 1). We also used additional survey data overlapping with our study area provided from pre- and post-construction monitoring of existing and proposed wind energy projects (Northwest Wildlife Consultants, unpublished reports) and other raptor monitoring efforts in the area (J. Watson, Washington Department of Fish and Wildlife, The Nature Conservancy, unpublished

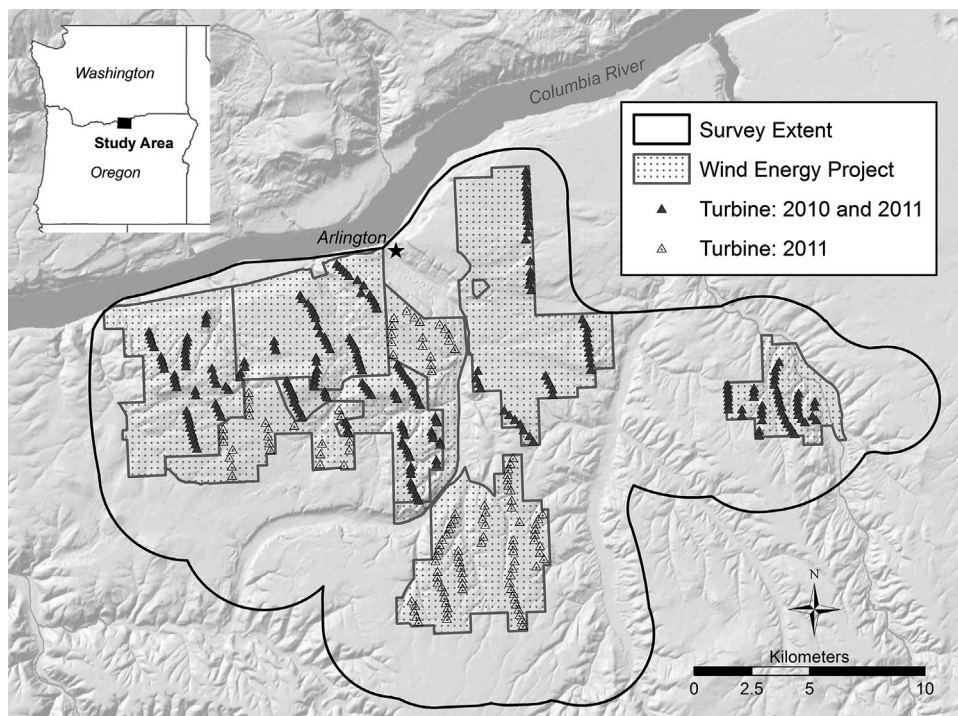


Figure 1. Area surveyed for breeding *Buteo* hawks in relation to individual wind energy projects and operational wind turbines during 2010 and 2011 in north-central Oregon, USA.

data) to locate breeding hawk pairs. We observed nests at a minimum distance of 250 m during brief, approximately 15–30-minute, observation periods to limit disturbance (Olendorff 1993) when possible.

We used modified definitions from Steenhof and Newton (2007) to define measures of reproduction for *Buteo* hawks. We used the term nesting area instead of nesting territory to avoid confusion with the ethological definition of a territory, which is based on an observed defensive behavior. We roughly delineate each nesting area using historical nesting information and species-specific buffers around the nest based on half the average nearest neighbor distance (NND) of breeding pairs documented in previous surveys of our study area (Northwest Wildlife Consultants and J. Watson, Washington Department of Fish and Wildlife, unpublished data). The average NND in the study area was reported to be 3.1 km for ferruginous hawks, 2.6 km for red-tailed hawks, and 1.7 km for Swainson's hawks, similar to published estimates for these species throughout their range in the Pacific Northwest (Fitzner 1980, Janes 1984, Bechard et al. 1990, Bechard and Schmutz 1995). We monitored nests every 7–10 days and considered them successful when ≥ 1 nestling reached 33 days old (i.e., $\geq 80\%$ of the average age at fledging for all 3 species; Bechard and Schmutz 1995, Preston and Beane 2009, Bechard et al. 2010) based on estimated ages from photographic guides (Mortisch 1983, 1985; Gossett and Makela 2005). We back-calculated from the ages of juveniles to estimate the hatching date and subtracted an additional 33 days for the average length of incubation (Bechard and Schmutz 1995, Preston and Beane 2009, Bechard et al. 2010) to estimate the laying date. We defined the post-fledging period as the time after fledging when juveniles voluntarily left the nest for the first time until they could no longer be located in the nesting area and were assumed to have reached independence.

We used a gradient-response design (Morrison et al. 2008) to select nests with young that were ≥ 33 days old for radio-marking. Under this design, we selected nests across a range of wind turbine distances and densities to investigate any potential indirect impacts to survival of young. We selected 25 nests each year and radio-marked 10 ferruginous hawks, 27 red-tailed hawks, and 23 Swainson's hawks to examine the potential for direct mortality from turbine collisions during the post-fledging period. We equipped ≥ 1 young from selected nests with a metal lock-on United States Geological Survey band and a 20-g backpack very high frequency (VHF) radio-transmitter secured by Teflon ribbon straps and a single copper crimp or sewn with cotton thread using methods described by Guetterman et al. (1991). We suspected that age rank within a brood may affect juvenile survival (Bechard 1983), but not sex (Zelenak et al. 1997). Consequently, for broods with >1 young, we alternately selected between the smallest and largest nestling at different age ranks, as determined by feather growth progression, without regard to sex. We conducted all handling, banding, and radio-marking techniques in compliance with Boise State University protocols for the Institutional Animal Care and Use Committee (IACUC number 006-AC10-006). We

checked transmitter signals and obtained visual locations of radio-marked fledglings 2–5 times/week. We assumed all fledglings that could not be located after extensive searching of the adult nesting areas and study area had reached independence. We continued to monitor all transmitter frequencies within the study area for the remainder of the season to determine if fledglings returned or were located in previously unknown areas. We determined sources of juvenile mortality and nest failure, when possible, by observing clues near nests and conducting field necropsies of carcasses.

We developed a priori hypothesis categories that we thought would influence nest success and post-fledging survival (Appendix A) based on previous raptor studies. The scale at which nesting pairs were influenced by many of these hypothesis categories was unknown, so we incorporated different distance and buffer measurements within each landscape-scale category that would be relevant to breeding adults at varying degrees within the average home range around the nest and could affect survival of fledglings indirectly. We also created one category that represented the influence of competition from nest-mates (brood size and age rank within brood) on post-fledging survival. However, because of low productivity across all species, we had few nests with 3 nestlings that reached 80% of fledging age and none with ≥ 4 nestlings of this age. As a consequence, we combined the second and third oldest ranking juveniles into one age rank category to compare against survival of the oldest. We calculated all spatial variables using geographic information system (GIS) techniques in ArcMap version 10.1 (Environmental Systems Research Institute, Redlands, CA, USA) and the Geospatial Modeling Environment (GME version 0.7.2.1, <http://www.spatialecology.com/gme/index.htm>, accessed 04 Sep 2012).

Covariates

We included temporal variables in our analyses to account for annual and seasonal fluctuations in nest success and post-fledging survival: year, hatch date, ordinal date, nest age, and fledgling age. We also included ordinal date (day 1 = 1 Jan) and the age of nests (day 1 = estimated initiation date) or radio-marked juveniles (day 1 = fledging date) as time-varying covariates where values were different on each calendar day. We used the mean species-specific initiation date for nests that failed during incubation. Finally, we considered 2 quadratic parameterizations of date and age because we predicted that survival would be greatest during the middle to late portion of the post-fledging period (e.g., Wiens et al. 2006) when fledglings are able to move to higher perches to avoid ground predation while still being provisioned by adults.

We included 2 landscape-scale measurements of wind turbines to account for their uneven spatial distribution and wide range of potential impacts to nearby nests: distance from the nest to the nearest wind turbine, and number of wind turbines within different radius intervals within the average home range size for these species. The mean core area used by nesting ferruginous hawks and red-tailed hawks

has been estimated at 35 km² and 15 km², respectively (Andersen and Rongstad 1989, Leary et al. 1998), and the home range of Swainson's hawks within the study area has been estimated at 17.2 km² (Watson et al. 2010). Therefore, we considered wind turbines densities within 1.6 km, 2.4 km, and 3.2 km of nests to be within the potential range of influence to breeding adults along an impact gradient.

We created 3 covariates to represent the potential negative influence of nearby breeding adults: the distance from each nest to the nearest breeding *Buteo* pair, distance to nearest conspecific pair, and the number of *Buteo* pairs within the average NND reported from our study area. The NND buffer included the number of *Buteo* nests within 1.5 km for ferruginous hawks, 1.2 km for red-tailed hawks, and 1.0 km for Swainson's hawks.

We created covariates with the percent of dominant land cover types within 1.6-km, 2.4-km, and 3.2-km radii around each nest to examine the impact of surrounding vegetation on nest success and juvenile survival. To determine the percent of each cover type surrounding nests, we used the 1:100,000 Ecological Systems map of Oregon (Oregon Natural Heritage Information Center 2010). We compared this map to observations in the field, and then edited the GIS dataset to reflect recent changes and combined land use and land cover types from the Oregon Land Cover Standard (Oregon Geospatial Enterprise Office 2010) into 4 broad categories: native (playa, shrubland, perennial grasslands), grass (non-native annual grasslands), agriculture (dryland wheat, fallow fields, early stage Conservation Reserve Program), and non-agricultural vegetation (native and grass categories combined).

Data Analysis

We determined the effect of explanatory covariates on nest success using a nest survival analysis to minimize potential biases associated with solely using the outcome of a nesting attempt (Steenhof and Newton 2007). We used the methods outlined by Rotella et al. (2004) and Stephens et al. (2005) to model the effect of variables on the daily survival rate (DSR) of *Buteo* hawk nests and radio-marked fledglings using PROC NLMIXED (SAS Institute, Cary, NC, USA). These models have also been recommended for telemetry data when monitoring intervals are uneven among samples and over time because the exact date of mortality is not typically known (Rotella et al. 2004). Therefore, nest survival models were ideal for estimating post-fledging survival of radio-marked juveniles as well because some dead birds were not located immediately and the fate of those with failed transmitters was not known definitively. We performed one analysis for the survival of all radio-marked fledglings combined and included an additive effect of species. However, we conducted a separate nest survival analysis for each hawk species to estimate nest success because we predicted that breeding adults would respond to covariates differently.

We used an information-theoretic approach to evaluate the effects of variables on the DSR of nests and radio-marked juveniles during the post-fledging period. We used a multi-

step modeling process to reduce the number of parameters in the final model set. First, we selected the best-approximating base model from the temporal hypothesis category to determine if survival remained constant or varied across the breeding season and with and without an additive effect of species. Next, we created models within each hypothesis category that included the standardized individual covariates with an additive effect of the top-ranking base temporal model. We evaluated the effects of wind turbine variables first and if the ratio of samples to parameters was sufficient (i.e., ~10:1; Burnham and Anderson 2002), we ranked models within other categories and selected the top model from each to compete in the final model set. If the top-ranking model within the hypothesis categories improved the fit of the base temporal model, we created further additive and interactive models to represent combinations of different hypotheses. We checked for multicollinearity among covariates in the final model set and found no evidence of correlation. Finally, we removed additive models that contained uninformative parameters (i.e., if they contained ≥ 1 additional covariate not found in higher-ranking models; Arnold 2010), resulting in the final model set.

We ranked models at each stage by Akaike's Information Criterion corrected for small sample sizes (AIC_c), and evaluated the strength of support for models at each stage using model weights (w_i) and the difference in AIC_c value (ΔAIC_c ; Burnham and Anderson 2002). We used model averaging to calculate the averaged parameter estimates and slope coefficients for models with a $\Delta AIC_c \leq 2.0$. Finally, we back-transformed the parameter estimates using the logistic equation and rescaled the standardized coefficients. We estimated the effect of each covariate using the slope coefficient ($\hat{\beta}$). We also evaluated the strength of the effect by the degree to which it overlapped 85% confidence intervals, allowing our results to be fully AIC compatible (Arnold 2010). We tested for evidence of overdispersion in the most highly parameterized and top-ranked models in all post-fledging survival analyses using the goodness-of-fit test outlined by Sturdivant et al. (2007) because nesting areas monitored in both years and radio-marked brood-mates may not have represented independent samples. We incorporated nesting area (unique identifier for each area) as a random effect in all models used to estimate nest success to account for this likely source of correlation (Rotella et al. 2004).

We estimated reproductive parameters as DSR^{*t*} based on the top model or model-averaged parameter estimates where *t* is the length of the period of interest. For nest success, *t* was equal to the number of days during incubation (33) and length of the nestling period to 80% of the average fledging age (33 days old). We used the same method to estimate survival for radio-marked fledglings prior to reaching independence, but the length of this period is variable among species and geographic areas in other studies (Bechard and Schmutz 1995, Preston and Beane 2009, Bechard et al. 2010). Therefore, we first tested for a species-specific difference in post-fledging period length using the non-parametric Kruskal-Wallis rank sums test in JMP version 10 (SAS Institute) and assessed all group means with

the Steel–Dwass test (Hsu 1996) following significant results. We examined outliers using boxplots, normal quantile plots, and the Shapiro–Wilk test to determine if the data were normally distributed.

Finally, we predicted that pairs arriving to the study area earlier would select higher quality nesting areas and initiate incubation first. Also, younger breeding pairs typically nest later and exhibit lower reproductive rates (Newton 1998, Espie et al. 2000), possibly because they are relegated to areas with greater mortality risks after older and more experienced breeding pairs select the optimum areas earlier (Carrete et al. 2006). In this context, we investigated whether the timing of nest initiation was related to wind turbines by fitting a linear model of the estimated hatch date of the oldest radio-marked fledgling per nest with the effect of wind turbine distance (log-transformed), species, and an interaction of these 2 variables. We examined outliers using boxplots, normal quantile plots, and the Shapiro–Wilk test to determine if the data were normally distributed, and fit these models in JMP version 10 (SAS Institute).

RESULTS

We documented nest failures for 6 (35%) of 17 ferruginous hawk, 4 (11%) of 35 red-tailed hawk, and 23 (34%) of 67 Swainson’s hawk breeding attempts. Nest failure appeared to result from a number of sources including predation of the nest or adults (18%), juniper removal (3%), and nests blown out of trees (15%), but most (58%) were abandoned or otherwise failed for unknown reasons with little variation in these causes among species. Adult Swainson’s hawks from 3 nests died as the result of collisions with turbines. Two of these nests failed and the third produced a single fledgling, which was radio-marked and successfully reached independence with provisioning from the remaining adult.

Nest Survival

The dataset for each species included 17 attempts at 12 nesting areas for ferruginous hawks, 35 attempts at 25 nesting areas for red-tailed hawks, and 67 attempts at 49 nesting areas for Swainson’s hawks. Because of the low

number of ferruginous hawk nests and low proportion of failed nesting attempts by red-tailed hawks, we included only wind turbine covariates with a random effect of nesting area for these 2 species to avoid over-parameterization (Burnham and Anderson 2002). We analyzed the full suite of models from hypothesis categories for the Swainson’s hawk nest survival analysis.

According to the model that assumed a constant DSR, the probability of nest success for the 66-day nesting period was 0.60 (85% CI = 0.45–0.82) for ferruginous hawks, 0.74 (85% CI = 0.60–0.92) for red-tailed hawks, and 0.62 (85% CI = 0.53–0.71) for Swainson’s hawks. However, this model was only well supported for red-tailed hawks (Table 1), indicating additional covariates helped explain the variation in nest success for the other 2 species. The top-ranking model for ferruginous hawks included the number of wind turbines within 3.2 km (32-km² area) and was well supported compared to the constant DSR model (Table 1). Daily survival rates for ferruginous hawk nests estimated from our survival models predicted success would decrease as the number of wind turbines within this home range buffer increased ($\hat{\beta} = -0.89$, SE = 0.39, 85% CI = -1.47 to -0.30; Fig. 2). The DSR of Swainson’s hawk nests was best explained by a quadratic age trend where survival was the highest during the early and late portions of the nesting period (Table 1). For example, the DSR of a 5-day-old nest and 45-day-old nest was 0.99 (85% CI = 0.99–1.00), but the DSR of a 25-day-old nest was 0.98 (85% CI = 0.96–0.99). The number of wind turbines within 1.6 km of nests was also in the top model for this species, but the model-averaged effect was not a reliable predictor of DSR ($\hat{\beta} = 0.36$, SE = 0.25, 85% CI = -0.01 to 0.73).

Post-Fledging Survival

The estimated mortality rate during the post-fledging period based on the species-only model was 30.0% for ferruginous hawks (3/10), 19.1% for red-tailed hawks (5/25, excluding the unknown fates of 2 fledglings with failed transmitters), and 17.0% for Swainson’s hawks (4/23). Six fledglings appeared to have been killed by mammalian or avian predators (i.e., 1 ferruginous hawk, 3 red-tailed hawks, and

Table 1. Ranking of nest survival models for each *Buteo* species in the Columbia Plateau Ecoregion of north-central Oregon, USA, 2010–2011. Model set reduced after removing those with uninformative parameters. Provided for each model is the Akaike’s Information Criterion adjusted for small sample sizes (AIC_c), Δ AIC_c for the *i*th model computed as AIC_c – min (AIC_c), AIC_c weight (w_i), the model likelihood [L in $-2\text{Log}(L)$], and the number of model parameters (K).

| Models ^a | AIC _c | Δ AIC _c | w_i | $-2\text{Log}(L)$ | K |
|---|------------------|---------------------------|-------|-------------------|-----|
| Ferruginous hawk | | | | | |
| Turb_3.2 km + nest | 47.07 | 0.00 | 0.79 | 41.04 | 3 |
| Intercept + nest | 49.68 | 2.61 | 0.21 | 45.66 | 2 |
| Red-tailed hawk | | | | | |
| Turb_1.6 km + nest | 35.05 | 0.00 | 0.64 | 29.02 | 3 |
| Intercept + nest | 36.17 | 1.11 | 0.36 | 32.15 | 2 |
| Swainson’s hawk | | | | | |
| Age + age ² + turb_1.6 km + nest | 173.07 | 0 | 0.50 | 163.03 | 5 |
| Age + age ² + nest | 173.37 | 0.30 | 0.43 | 165.35 | 4 |
| Intercept + nest | 177.07 | 4.01 | 0.07 | 175.07 | 1 |

^a Covariates were defined as follows: turb_3.2, 2.4, and 1.6 km, density of wind turbines within each radius interval of the nest; age + age², time-varying survival based on quadratic age of the nest since estimated incubation; nest, random effect of nest area.

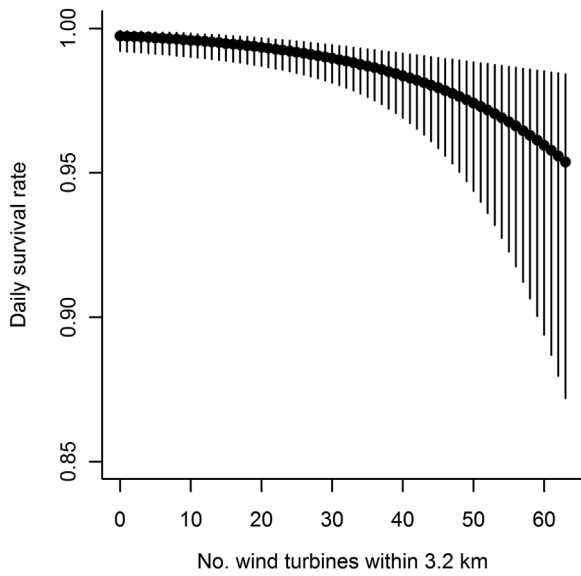


Figure 2. Influence of the number of wind turbines within 3.2 km of ferruginous hawk nests in the Columbia Plateau Ecoregion of Oregon, USA during 2010 and 2011 on the daily survival rate (DSR) across the nesting period (66 days). Solid dots represent the mean survival rate and lines represent 85% confidence intervals.

2 Swainson’s hawks). Four fledglings appeared to have died from starvation or disease (i.e., 1 ferruginous hawk, 2 red-tailed hawks, and 1 Swainson’s hawk). One Swainson’s hawk also drowned in a stock tank. Approximately, half of the selected radio-marked fledglings were potentially vulnerable to collisions during the post-fledging period because they were hatched from nests within 800 m of an operating wind turbine, which is within the average natal range (i.e., 2.01 km²; Fitzner 1980, Pope 1999). However, although sources of mortality for radio-marked fledglings varied, no fatalities were found under wind turbines and thus

were not attributed to collisions. Dead fledglings could have been moved by scavengers, but we thoroughly searched under nearby turbines and found no sign of feathers or remains that would indicate such a scenario. The mean number of days between the last observation of fledglings alive to the first day they were found dead was 3 days (range = 1–11 days).

We documented 2 transmitter failures for red-tailed hawk fledglings early after deployment in 2011 and were unable to determine the fate of these individuals. However, we were able to locate them visually within the natal range until the average age of independence and used these data in estimating the DSR. Also, 2 radio-marked juvenile ferruginous hawks from the same nest did not technically die during the post-fledging period (after fledging and before independence) but were included in the survival analysis because of their relative age at death. They appeared to have been abandoned by the adults and had not yet reached independence. The younger of the 2 was killed by siblicide prior to leaving the nest although it was within the average fledging age. The brood-mate of this juvenile successfully fledged, but appeared to leave the natal range and study area after only 5 days and was found dead of apparent starvation approximately 8 km away from the nest 11 days later. Siblicide of older nestlings was documented at other nests of all 3 species but was difficult to confirm in some cases.

For those radio-marked juvenile *Buteo* hawks that survived to independence, we found differences among species in the length of the post-fledging period (Kruskal–Wallis $\chi^2_2 = 12.06$, $P = 0.002$). Ferruginous hawks had the shortest mean length of the post-fledging period ($n = 8$, $\bar{x} = 20.75 \pm 3.30$ days) and the period was different from red-tailed hawks ($Z = 2.99$, $P = 0.008$), but not from Swainson’s hawks ($Z = 3.23$, $P = 0.36$). The post-fledging period was longer ($Z = -2.54$, $P = 0.03$) for red-tailed hawks ($n = 20$, $\bar{x} = 31.60 \pm 2.09$ days) compared to Swainson’s hawks ($n = 18$, $\bar{x} = 26.56 \pm 1.14$ days).

Table 2. Ranking of additive and interactive models used to examine factors influencing post-fledging survival of radio-marked *Buteo* species in the Columbia Plateau Ecoregion of north-central Oregon, USA, 2010–2011. Model set reduced after removing those with uninformative parameters. Provided for each model is the Akaike’s Information Criterion adjusted for small sample sizes (AIC_c), ΔAIC_c for the i th model computed as $AIC_c - \min(AIC_c)$, AIC_c weight (w_i), the model likelihood [L in $-2\text{Log}(L)$], and the number of model parameters (K).

| Model ^a | AIC _c | ΔAIC_c | w_i | $-2\text{Log}(L)$ | K |
|--|------------------|----------------|-------|-------------------|-----|
| Age + age ² + spp + turb_2.4 km + buteo_d + grass_2.4 km + rank | 96.17 | 0.00 | 0.51 | 77.99 | 9 |
| Age + age ² + spp + turb_2.4 km + buteo_d + grass_2.4 km | 97.80 | 1.63 | 0.22 | 81.66 | 8 |
| Age + age ² + spp + turb_2.4 km + grass_2.4 km | 99.42 | 3.25 | 0.10 | 85.31 | 7 |
| Age + age ² + spp + grass_2.4 km | 100.86 | 4.68 | 0.05 | 88.77 | 6 |
| Age + age ² + spp + turb_2.4 km × grass_2.4 km | 101.23 | 5.06 | 0.04 | 85.09 | 8 |
| Age + age ² + spp + turb_2.4 km × buteo_d | 102.02 | 5.84 | 0.03 | 85.87 | 8 |
| Age + age ² + spp + turb_2.4 km + buteo_d | 102.71 | 6.53 | 0.02 | 88.60 | 7 |
| Age + age ² + turb_2.4 km + buteo_d | 104.54 | 8.37 | 0.01 | 88.39 | 8 |
| Age + age ² + spp + turb_2.4 km | 104.77 | 8.60 | 0.01 | 92.69 | 6 |
| Age + age ² + grass_2.4 km | 104.78 | 8.61 | 0.01 | 96.74 | 4 |
| Age + age ² + spp + turb_2.4 km | 106.00 | 9.83 | 0.00 | 91.89 | 7 |
| Age + age ² + spp + buteo_d | 106.09 | 9.91 | 0.00 | 94.00 | 6 |
| Age + age ² + spp | 106.26 | 10.08 | 0.00 | 96.20 | 5 |
| Age + age ² | 107.23 | 11.05 | 0.00 | 101.20 | 3 |
| Intercept | 124.33 | 28.16 | 0.00 | 122.33 | 1 |

^a Covariates were defined as follows: age + age², time-varying survival based on quadratic age at fledging; spp, categorical species variable; turb_2.4, density of wind turbines within 2.4 km of the nest; buteo_d, distance from a nest to the nearest breeding *Buteo* pair; grass_2.4 km, percentage of grassland vegetation within 2.4 km of the nest; rank, categorical rank of broodmates based on relative age at capture.

Survival during the post-fledging period was species-specific, varied by age, and was influenced by surrounding landscape variables (Table 2). We found no evidence of overdispersion with the goodness-of-fit test of the global model from AIC_c model selection ($P \geq 0.10$ in both cases). Therefore, we assumed that the fates of radio-marked juveniles were independent and did not include a random effect in post-fledging survival models. Consistent with our predictions, we found a strong quadratic effect of age on DSR of radio-marked fledglings for all 3 species; survival was lowest for younger juveniles during the first few days after fledging and also for older juveniles just prior to independence. The global model and a model with one less variable, brood age rank, contained 76% of the total model weight and were averaged for inference. The model-averaged effect of

the number of wind turbines within 2.4 km of the nest was negative for all 3 species ($\hat{\beta} = -1.13$, SE = 0.22, 85% CI = -1.81 to -0.45), but the effect of this variable was strongest for ferruginous hawks (Fig. 3; Table 3). The percentage of exotic grassland habitat in a 2.4-km buffer ($\hat{\beta} = 0.93$, SE = 0.20, 85% CI = 0.30–1.57), distance to the nearest *Buteo* nest ($\hat{\beta} = -0.88$, SE = 0.18, 85% CI = -1.49 to -0.28) and brood age rank ($\hat{\beta} = -1.11$, SE = 1.08, 85% CI = -2.61 to 0.38) were also included in the best-approximating models (Fig. 3), but model-averaged estimates of rank were unreliable predictors for our data. Given the quadratic effect of age in our models, we estimated survival over the median species-specific length of the post-fledging period, each at 3 densities of wind turbines within 2.4 km of the nest (Table 3).

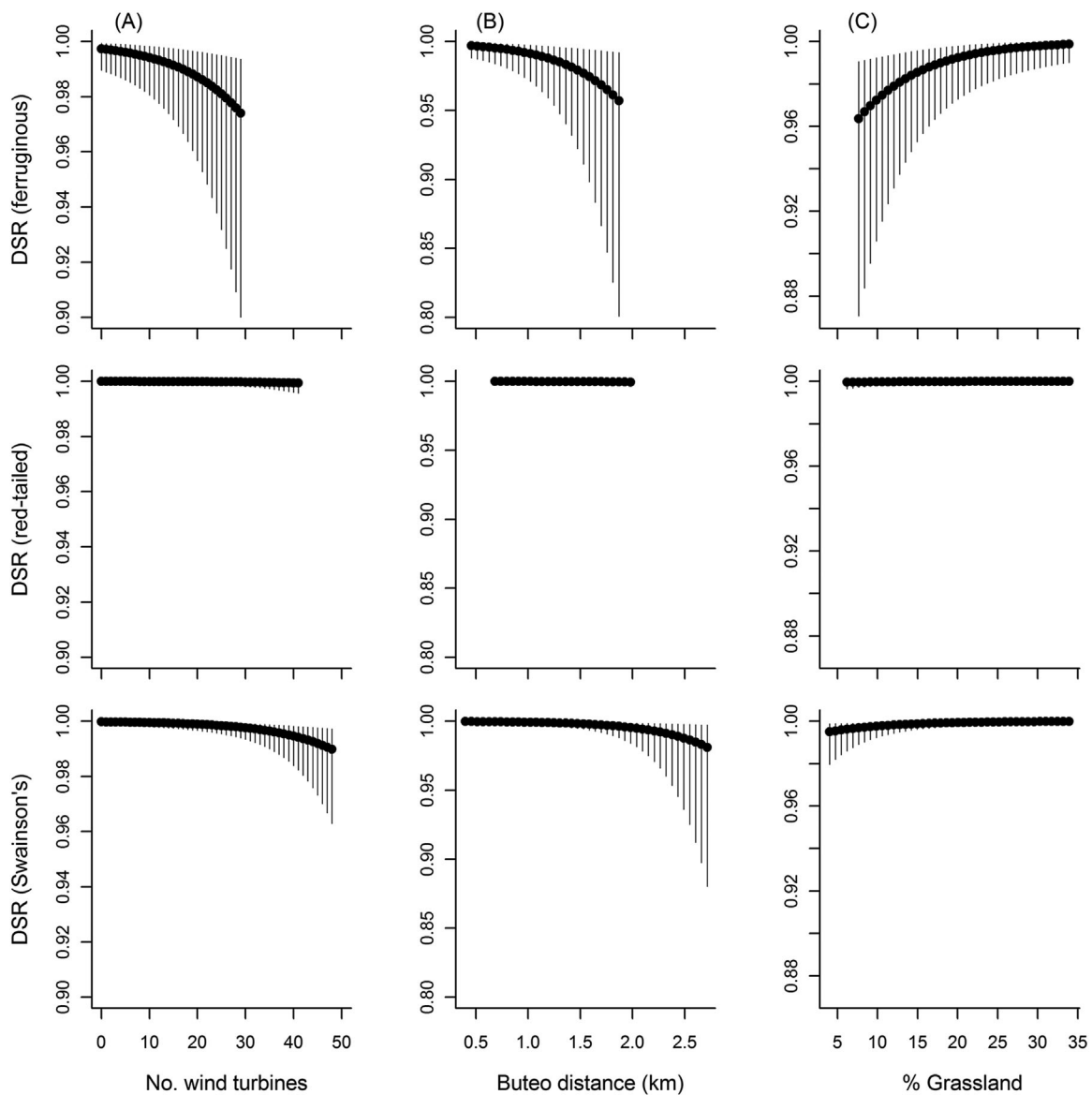


Figure 3. Relationship of covariates on the predicted daily survival rate (DSR) for a 55-day-old radio-marked *Buteo* hawk in the Columbia Plateau Ecoregion of Oregon, USA in 2010 and 2011. Displayed is the DSR as an additive combination of a random effect of nest area with all other variables fixed at mean values for column: (A) density of wind turbines within 2.4 km of the nest, (B) distance from the nest to the nearest breeding *Buteo* pair (km), and (C) percentage of grassland vegetation within 2.4 km of the nest. Solid dots represent the mean DSR and lines represent 85% confidence intervals.

Table 3. Probability of surviving the median post-fledging period at zero (low), 50th (mid), and 90th (high) percentiles of wind turbines within 2.4 km of the nest for radio-marked juvenile *Buteo* hawks in north-central Oregon, USA, 2010–2011 with 85% confidence intervals. Predicted survival from the median age at fledging to independence is estimated as the product of the daily post-fledging survival rates based on the top-ranking model-averaged parameter estimates.

| <i>Buteo</i> species | Turbine density within 2.4 km | Predicted survival |
|--|-------------------------------|-------------------------------|
| Ferruginous hawks (Age range = 44–65) | | (21-day post-fledging period) |
| | Low: 0 | 0.85 (0.57–0.96) |
| | Mid: 10 | 0.71 (0.35–0.89) |
| | High: 20 | 0.49 (0.10–0.79) |
| Red-tailed hawks (Age range = 41–73) | | (32-day post-fledging period) |
| | Low: 0 | 0.99 (0.95–1.00) |
| | Mid: 20 | 0.98 (0.89–1.00) |
| | High: 38 | 0.92 (0.67–0.98) |
| Swainson’s hawks (Age range = 44–71) | | (27-day post-fledging period) |
| | Low: 0 | 0.98 (0.91–1.00) |
| | Mid: 20 | 0.93 (0.80–0.97) |
| | High: 38 | 0.72 (0.40–0.89) |

Hatch Date and Turbine Distance

We found a significant difference in the estimated hatch date of radio-marked fledglings for the interaction of species and log wind turbine distance ($F_{(0.05) 5, 44} = 69.12, P < 0.001$). Wind turbine distance was positively related to hatch date for red-tailed hawks ($P = 0.003$; Fig. 4). Breeding ferruginous hawks ($P = 0.06$) and Swainson’s hawks ($P = 0.26$) farther from turbines nested earlier, but this was only a weak non-significant relationship.

DISCUSSION

Buteo hawks in our study appeared to be sensitive to the density of wind turbines during the breeding season. Despite the concern that fledglings may have a high risk of collision mortality, however, we found no evidence that they were directly killed by turbines in our study area. We postulate this is because of the low overall activity of the radio-marked fledglings, the limited size of their natal home range, and the relatively short duration of exposure to wind turbines during the 3–4-week post-fledging period when fledglings typically perched or engaged in short, low flights below the rotor-swept zone. All of these factors likely contributed to a lower probability of fledglings encountering a turbine; this is in contrast to adults that are more active and wide-ranging during the multi-month breeding season and could therefore be expected to have a higher frequency of turbine collisions. Recent post-construction fatality monitoring conducted in and around wind facilities during the breeding season (Northwest Wildlife Consultants, unpublished reports), and other fatalities found incidentally during this study indicate that adults and sub-adults sustain the most collision mortality of *Buteo* hawks instead of juveniles. This finding is important because it has been suggested that fledglings

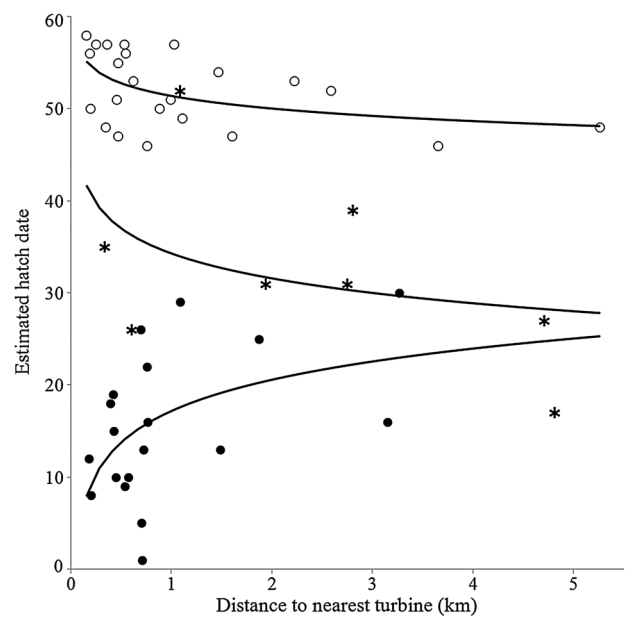


Figure 4. Relationship between estimated hatch date of the oldest nestling and log-transformed distance from the nest to the nearest wind turbine (km) for each species of *Buteo* hawk in north-central Oregon, USA, 2010–2011. Ferruginous hawks are represented by asterisks, red-tailed hawks by closed circles, and Swainson’s hawks by open circles.

have a greater risk of collision mortality compared to other ages and life-history stages (Barrios and Rodriguez 2004, Carrete et al. 2009), but this may only be the case for those species with longer post-fledging periods, or for dispersing juveniles after reaching independence from adults.

We found that greater wind turbine densities were related to decreased nest success for ferruginous hawks and lower survival of *Buteo* fledglings, but the specific mechanisms driving these relationships were unclear. Blade-strike fatalities of raptors are thought to be the primary negative effect of wind energy development (Carrete et al. 2009), and collision risk can depend upon a wide range of site-, season-, and species-specific factors. Resident (rather than migrating) raptors, in particular, may be more susceptible to collisions with wind turbines. This is likely because local movements (e.g., hunting prey, defending a territory against conspecifics) confer a greater likelihood of risk-prone flights within the rotor-swept zone (Smallwood et al. 2009, Katzner et al. 2012, Marques et al. 2014). Collision risk and the subsequent effect on reproduction may be greatest for adults during the breeding period, but this impact could affect species differently. Dahl et al. (2012), for example, reported that collisions with turbines by white-tailed eagles (*Haliaeetus albicilla*) in Norway peaked during the early breeding period when flight activity near wind turbines was the greatest. This additional source of mortality ultimately led to the vacancy of historical nesting areas, which in turn lowered breeding success in areas closer to turbines after construction (Dahl et al. 2012). The risk of collisions for red kites (*Milvus milvus*) was also reported to be greater when breeding pairs nested closer to wind turbines (Eichhorn et al. 2012) and in greater densities of wind turbines (Schaub 2012).

Conversely, Hernández-Pliego et al. (2015) reported few fatalities of Montagu's harriers (*Circus pygargus*) in Spain, and no adverse effects from wind turbine distance on nest or colony abundances after construction.

A comparison of observed mortality rates between our study area and the broader region also suggests interspecific variability in the risk of collisions with wind turbines. For example, Swainson's hawks and ferruginous hawks comprised only a small portion of all raptor species reported from fatality monitoring at wind energy projects elsewhere in the CPE (9% and 4%, respectively), as compared to red-tailed hawks (22%; Johnson and Erickson 2011). Conversely, in our study area, the majority of raptor fatalities found during post-construction fatality monitoring and incidentally by our surveys was Swainson's hawks (45%), as compared to fewer ferruginous hawks (10%) and red-tailed hawks (8%; Northwest Wildlife Consultants, unpublished reports). Our nest success and post-fledging survival results differ from these findings in that we observed the greatest negative effect of turbine density on ferruginous hawks, as opposed to the other 2 species.

Rather than turbine collisions being a single proximate cause of decreased nest success and high post-fledging mortality of juvenile hawks, we posit that our results represent a species-specific combination of breeding adults being killed by turbine collisions and indirectly disturbed and displaced from portions of their home range by activities associated with the increasing wind energy development in the area. A recent review of studies examining indirect impacts from wind turbines concluded that disturbance near wind energy facilities can displace some avian species from accessing resources (May 2015). Few authors, however, have related these effects to the intensity of development (e.g., wind turbine variables used in our study). The fact that we found some breeding pairs nesting in areas with high densities of wind turbines suggests they were habituated to the noise and activity of the rotating blades. However, they may have responded to other types of intermittent activities that invoked abrupt and stress-related behaviors (e.g., fleeing in response to operations and maintenance associated with the facility or infrastructure [Madders and Whitfield 2006], impulsive evasion of turbine blades in flight [Garvin et al. 2011, May 2015]). This may have been especially true for the ferruginous hawks in our study because this species increases defense behavior (Keeley and Bechard 2011) and flushes at greater distances with consecutive disturbances near the nest, suggesting they may be particularly sensitive to operations and maintenance activities (White and Thurow 1985, Keeley and Bechard 2011). Repeated exposure to such stimuli can alter flight trajectories or disrupt foraging and nesting behaviors, ultimately leading to changes in habitat use within the home range relative to the spatial configuration of nearby turbines or operational activities (Farfán et al. 2009, Pearce-Higgins et al. 2009, May 2015). The extent of such displacement would depend upon the perceived risk of mortality while foraging and flying near turbines versus the availability of suitable alternative habitats nearby (May 2015). Breeding adults

that choose to nest in areas with turbines may have a greater risk of collision mortality because of the increased frequency of flights necessary to provision young. Increased vigilance can minimize the probability of collisions through anticipatory evasion, depending upon many factors such as the level of natural awareness and perception of risk, but at the cost of reduced time or altered daily patterns for normal activities (May 2015). Alternatively, breeding pairs may seek out other sources of prey in areas with lower short-term survival costs that are farther away, requiring more energetically expensive flight.

The consequences of these direct and indirect effects of wind energy development on adults in our study appear to have manifested at multiple stages in the breeding cycle. For example, even though no radio-marked fledglings were killed from collisions, juveniles from nests near greater densities of wind turbines were more likely to die by predation or starvation just after fledging and prior to reaching independence. Also, a large proportion of the failed nests and some fledglings appeared to have been abandoned for unknown reasons, especially among ferruginous hawks in areas of greater wind turbine density. The apparent abandonment and incidence of siblicide in older marked and un-marked nestlings that we observed is rare in *Buteo* hawks (White and Thurow 1985, Bechard and Schmutz 1995). These sources of juvenile mortality are usually indicative of reduced provisioning or decreased prey availability (Bechard 1983, Estes et al. 1999), but we did not quantify these measures and our coarse-scale land cover variables were probably not sufficient surrogates. However, although the sources of nest failure and mortality could be related to natural variation in the seasonal availability or spatial distribution of prey, the death of even one pair member or the displacement of adults within the home range could also reduce the provisioning rate and affect other important aspects of parental care, resulting in the loss of dependent young (Schmutz et al. 2014). This could have been the case in our study if breeding adults were killed by wind turbines or disturbed and displaced by development activities.

Other factors such as variation in the quality of nesting areas across the study area could have influenced our results. For example, pairs nesting in areas with greater densities of wind turbines might be predisposed to a higher rate of failure and post-fledging mortality if these developments were already constructed outside of optimal nesting and foraging areas. The fact that post-fledging survival was higher in areas with larger percentages of grassland vegetation and farther from conspecifics suggests some natural variation in quality across the landscape. Under many circumstances, higher quality nesting areas generally support a greater number of breeding pairs (Schmutz 1989) meaning wind turbines, surrounding vegetation, and conspecific distance could have been confounded with one another in our study. However, the density of pairs alone may not be sufficient to assess the quality of nesting habitats (Newton 1998), especially in areas with sudden environmental change that may alter an individual's ability to evaluate the true quality of an area as it relates to survival and reproduction (Robertson and

Hutto 2006, May 2015). Interaction models with these variables also had little support and we found no evidence that pairs closer to turbines initiated nesting later than those farther away, which would be expected if breeding hawks viewed nesting areas near wind turbines as lower quality. To the contrary, red tailed hawks were the least affected from wind turbines, but those nesting closer to them did so significantly earlier than those farther away, suggesting they were the first areas chosen during the pre-nesting period. In a separate analysis, we report that the occurrence of breeding pairs was not related to wind turbine distance or density, indicating they were not displaced from selecting nests at larger spatial scales in these areas during our 2-year study (Kolar 2013). However, it will be necessary to study longer term trends in occupancy and reproduction to determine if the negative effects of wind turbines persist. High fidelity to historical territories could mean pairs would continue to return to the same nesting areas regardless of collisions or indirect effects and potentially suffer reduced reproduction in the short-term, but also might be less likely to be replaced after death (Drewitt and Langston 2006).

MANAGEMENT IMPLICATIONS

Our results underscore the need to consider the direct and indirect effects of wind energy development and natural sources of variation on raptors at ecologically relevant spatial scales (e.g., within the home ranges of local resident pairs of hawks). In general, future wind energy projects should limit the construction of wind turbines in raptor nesting areas, especially when occupied by a species with special conservation status or sensitive to human disturbance (e.g., the ferruginous hawk), and in habitats that contribute to greater reproductive success. Collision fatalities can be reduced by adjusting the placement of specific turbines (de Lucas et al. 2012), but the potential for indirect impacts based on turbine density necessitate that planning of future wind energy facilities consider these effects at larger geographic scales beyond individual turbines to determine the cumulative impacts to raptor populations (Schaub 2012). Individual wind energy projects can potentially have a disproportionate impact if not well-sited, something we were unable to fully evaluate in our study because 44% of the home range buffers overlapped with turbines from 2 or more facilities. However, it appeared that lower densities of wind turbines had a minimal impact on reproductive parameters for the 3 *Buteo* species in our study. We caution that the applicability of our results to the nesting success of the broader breeding population is ultimately unknown because of our non-probabilistic sampling design. Nonetheless, our results did suggest that indirect impacts to reproduction of hawks spatially associated with wind energy facilities may occur via reductions in nest success and post-fledging survival rates. Understanding the ways in which different segments of wildlife populations are affected by wind energy development and the extent of any impacts should help guide regional planning to better integrate future wind energy developments into the landscape.

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APPENDIX A

Description of candidate models used to assess variation in nest success and post-fledging survival for ferruginous hawks, red-tailed hawks, and Swainson's hawks in the Columbia Plateau Ecoregion of north-central Oregon, USA, 2010–2011.

| Hypothesis category | Model name | Model description |
|------------------------------------|-----------------------------------|---|
| Base model and temporal covariates | Intercept | Null model indicating that DSR is constant (i.e., no effect) |
| | Spp ^a | Survival varies by species |
| | Age and age ² | Time-varying survival based on the age or quadratic age of a nest or at fledging |
| | Date and date ² | Time-varying survival based on the ordinal date or quadratic date at fledging |
| | Hatch ^a | Estimated ordinal hatch date based on oldest nestling |
| | Year | Annual changes in survival |
| | Spp + age or age ^{2a} | Time-varying age or quadratic age by species |
| | Spp + date or date ^{2a} | Time-varying date or quadratic date by species |
| | Spp + hatch ^a | Ordinal hatch date by species |
| | Spp + year ^a | Annual survival by species |
| Landscape models | | |
| Wind turbines | Turb_dist | Continuous distance from occupied nest to nearest wind turbine |
| | Turb_1.6 km or 2.4 km or 3.2 km | Density of turbines at each radius interval surrounding nest |
| Land cover | | |
| | Ag_1.6 km or 2.4 km or 3.2 km | Percent of intensively managed agriculture at each radius surrounding nest |
| | Native_1.6 km or 2.4 km or 3.2 km | Percent of native grassland and shrubland vegetation at each radius surrounding nest |
| | Grass_1.6 km or 2.4 km or 3.2 km | Percent of non-native annual grassland vegetation at each radius surrounding nest |
| | NonAg_1.6 km or 2.4 km or 3.2 km | Percent of non-agricultural vegetation (native and exotic grasslands) at each radius surrounding nest |
| Nearest <i>Buteo</i> neighbor | | |
| | Buteo_d | Distance to nearest adjacent <i>Buteo</i> nest |
| | Consp_d | Distance to nearest adjacent conspecific nest |
| | Buteo_NND | Number of occupied <i>Buteo</i> nests within the average nearest neighbor distance for each species |
| Nest-mate ^a | | |
| | Brood | Number of young in each brood that survive to fledging age |
| | Rank | Age rank in brood (oldest vs. all others) from young that survive to fledging age |
| Random effects models ^b | | |
| | Nest | Random effect of nesting area (unique identifier for each area) |

^a Model used in post-fledging survival analysis only.

^b Model used in nest survival analysis only.