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Research Article

Human-Made Structures, Vegetation, and Weather Influence Ferruginous Hawk Breeding Performance

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ABSTRACT Studies of anthropogenic impacts on wildlife may produce inconclusive or biased results if they fail to account for natural sources of variation in breeding performance and do not use probabilistic sampling at a scale functional for management. We used stratified random sampling and generalized linear mixed models to test hypotheses on relationships of daily nest survival rate (DSR) and fledgling production with anthropogenic and environmental factors that influence reproduction in the ferruginous hawk (*Buteo regalis*). We conducted the study across ferruginous hawk range in Wyoming, USA, 2010–2012. We performed extensive field surveys of prey, vegetation, and nest substrates, and used spatially explicit data to quantify weather, and the most widespread forms of anthropogenic infrastructure (i.e., roads, oil and gas well pads) in ferruginous hawk territories. We found strong evidence that DSR and productivity were greater for nests on anthropogenic structures (i.e., artificial nest platforms, gas condensation tanks, abandoned windmill platforms, power poles) compared to natural substrates (i.e., trees, cliffs, rock outcrops). Additionally, ferruginous hawks produced more fledglings at territories with greater shrub cover and fewer severe storms during the June brood-rearing period. Amount of oil and gas development and prey was not associated with either measure of breeding performance. Our results suggest that artificial nest platforms are an effective tool to improve breeding success of ferruginous hawks and nesting on anthropogenic structures does not constitute an ecological trap for this species. Although ferruginous hawks nested in some areas with very little vegetative cover, territories with greater amounts of shrub cover produced more fledglings. The negative impact of severe spring storms on fledgling production illustrates the importance of including future weather scenarios in management planning for this species because storms are predicted to increase in frequency and intensity as a result of climate change. Published 2015. This article is a U.S. Government work and is in the public domain in the USA.

KEY WORDS anthropogenic infrastructure, artificial nest platform, *Buteo regalis*, ferruginous hawk, fledgling production, nest survival, oil and gas development, prey abundance, severe weather, Wyoming.

Breeding success of birds is influenced by numerous factors, including composition and configuration of the surrounding landscape (Rodewald 2002), nest substrate and placement (Roth and Marzluff 1989), weather and climate (Dreitz et al. 2012), food availability (Steenhof et al. 1997), predation risk (Chalfoun et al. 2002), natural (Rota et al. 2014) and anthropogenic (Beale and Monaghan 2004) disturbance, and nesting stage (Stanley 2000). Studies intended to isolate management-relevant variables can produce inconclusive or biased results if they fail to account for important competing sources of variation. It is, therefore, critical to evaluate a full suite of relevant anthropogenic and environmental factors in models of habitat selection (Fedy et al. 2014) and breeding success of birds (McIntyre and Schmidt 2012). This is not a new concept (Kennedy 1980), but environmental impact studies rarely evaluate the effect of a disturbance within the context of the historical range of variability caused by natural processes (Morgan et al. 1994, Schueck and Marzluff 1995). Additionally, many studies evaluating effects of disturbance

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on wide-ranging wildlife, such as raptors, are not conducted at scales functional for management (Poiani et al. 2000, Wiens 2009) or appropriate to the broad extent typical of anthropogenic landscape modification (Copeland et al. 2009, van der Ree et al. 2011).

The ferruginous hawk (*Buteo regalis*) is a species of conservation concern (U.S. Fish and Wildlife Service 1992, Committee on the Status of Endangered Wildlife in Canada 2008, Wyoming Game and Fish Department 2010) that nests in grassland and shrubland habitats of the western United States and Canada (Bechard and Schmutz 1995) currently undergoing extensive modification from oil and gas development (Copeland et al. 2011, Allred et al. 2015). Although oil and gas development has had negative impacts on breeding success of some bird species (Naugle et al. 2011, Hethcoat and Chalfoun 2015, Ludlow et al. 2015), studies on the response of ferruginous hawks are equivocal. Loss and fragmentation of native habitat (Coates et al. 2014) by oil and gas development (Harmata 1991, Keough 2006) and agriculture (Schmutz 1987) have negatively affected breeding success of ferruginous hawks, possibly because of the sensitivity of this species to disturbance at nest sites (White and Thurow 1985, Keeley and Bechard 2011). Ferruginous hawks may, however, benefit from other anthropogenic modifications of their habitat, including some types of roads (Gilmer and Stewart 1983, MacLaren et al. 1988), increased abundance of prey in edge habitats (Zelenak and Rotella 1997, Keough and Conover 2012), and anthropogenic structures for perching and nesting (Steenhof et al. 1993, Keough and Conover 2012), including nest platforms installed for habitat enhancement and mitigation (Tigner et al. 1996). Habitat selection and breeding performance of ferruginous hawks are also influenced by natural factors, including vegetative cover (Keinath et al. 2010), prey abundance (Smith et al. 1981, Schmutz et al. 2008), congeneric competition (Restani 1991), spring weather (Gilmer and Stewart 1983), and availability of nesting substrates (Kennedy et al. 2014). Continued expansion of energy development in grassland and shrubland habitats has created a pressing need to inform land managers with a better understanding of the relative importance of anthropogenic and environmental factors in the ecology of ferruginous hawks.

Our primary objective was to determine the most important influences on breeding success of ferruginous hawks by evaluating anthropogenic and environmental factors known to affect performance of raptor populations. An additional goal was to make inference over a broad spatial extent relevant to management by randomly sampling the full breeding distribution of ferruginous hawks in Wyoming, and using methods to account for imperfect detection.

We tested predictions about the relationship of daily nest survival rate (DSR) and fledgling production with covariates representing prey abundance, vegetative cover, weather, degree of anthropogenic infrastructure (i.e., roads, oil and gas well pads), and nest substrates. We predicted DSR and fledgling production would be positively related to prey abundance because occupancy and productivity of ferruginous hawks increase when mammalian prey are abundant and available (Smith et al. 1981, Schmutz et al. 2008). Ferruginous hawks occur in sparsely vegetated areas across their distribution (Bechard and Schmutz 1995), including Wyoming (Keinath et al. 2010); we predicted DSR and fledgling production would be higher in territories more characteristic of habitat with less vegetative cover. We predicted both response variables would be negatively related to precipitation amount, number of storms, and lower minimum temperatures because cold spring weather and precipitation would increase physiological stress for breeding hawks and nestlings, leading to nest abandonment and reduced productivity (Sergio 2003, Kostrzewa and Kostrzewa 2008). Accordingly, we predicted average maximum daily temperature would be positively related to response variables early in the breeding season but negatively related later in the season (i.e., Jun of warmer years) because nestling Buteo hawks experience heat stress (Tomback and Murphy 1981, Kirkley and Gessaman 1990). We predicted DSR and fledgling production would be lower for sites nearer to roads and active well pads because oil and gas infrastructure and associated activities, which are rapidly expanding in Wyoming (Copeland et al. 2009), could disturb nesting behavior and habitat (White and Thurow 1985, Harmata 1991, Keough 2006), and roads could fragment habitat and facilitate anthropogenic disturbance (Olendorff 1993, Martínez-Abraín et al. 2010, Smith et al. 2010, Coates et al. 2014). Finally, we predicted nests on anthropogenic structures would have greater DSR and fledgling production than those on natural substrates because higher rates of occupancy and productivity have been documented for ferruginous hawks nesting on artificial platforms (Schmutz et al. 1984, Tigner et al. 1996, Neal et al. 2010, Wallace 2014) and other anthropogenic structures (Gilmer and Stewart 1983, Steenhof et al. 1993).

STUDY AREA

Our study area was the distribution of ferruginous hawks in Wyoming, USA (Keinath et al. 2010; Fig. 1). This 114,217-km^2 area comprised approximately 45% of the state, and was dominated by lowland sagebrush steppe habitat of the Wyoming Basin ecoregion and prairie habitat of the Great Plains ecoregion (Chapman et al. 2004). Mean annual precipitation ranged from 15 cm to 40 cm, and elevation from 1,000 m to 2,000 m (Knight 1996). Land ownership was 51% private, 37% Bureau of Land Management (BLM), 6% State, 0.7% Department of Agriculture, and 5.3% other.

METHODS

Nest Monitoring

During spring 2010 and 2011, we used fixed-wing aircraft to survey raptor nests in a random sample of 104 of 1,230 United States Public Land Survey System townships with centroids in our study area. We stratified our study area by 3 densities of active oil and gas wells (i.e., none: 0 wells; low: 1–30 wells; and high: >30 wells) and sampled an equal number of townships from each strata to capture the range of development intensity across Wyoming. We surveyed each 93.3-km^2 township with 16 parallel north-south

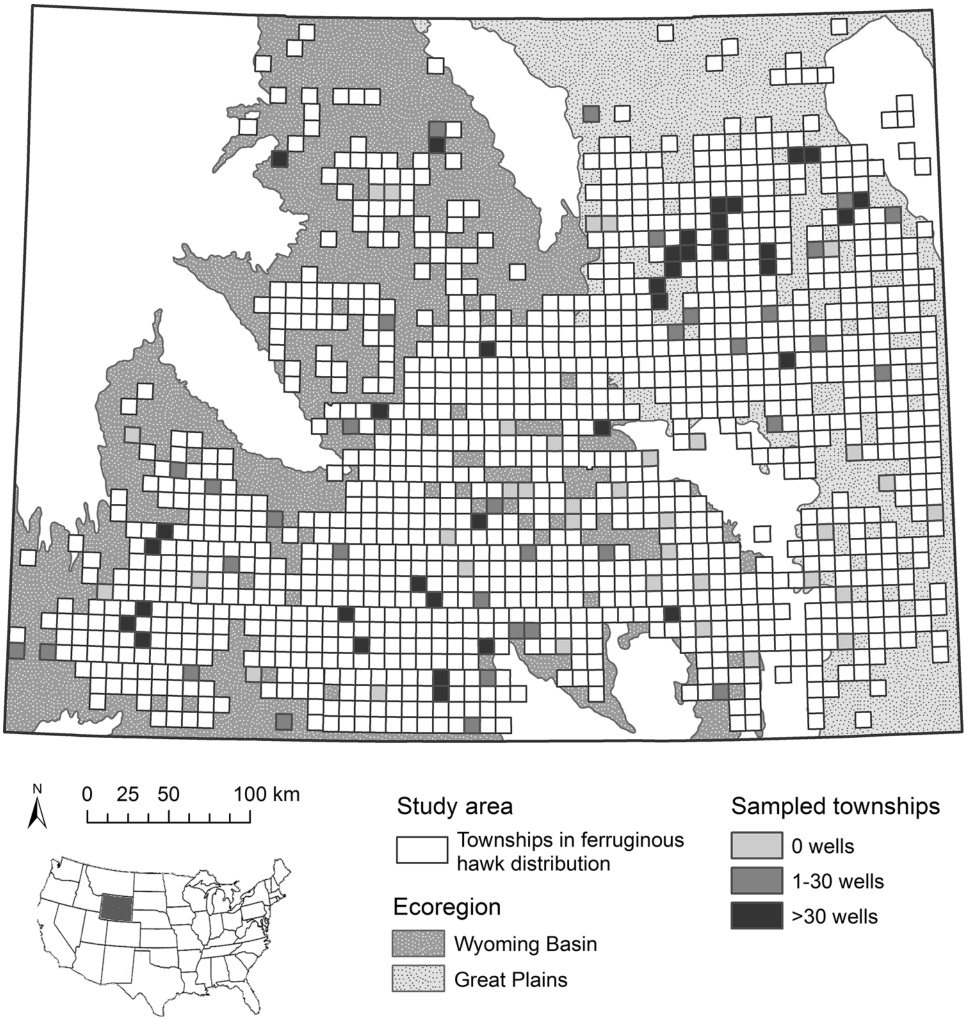

Figure 1. Study area encompassing the distribution of ferruginous hawks in Wyoming, USA. Depicted are Public Land Survey System townships with centroids in the study area, townships sampled for ferruginous hawk nests stratified by 3 levels of oil and gas well density, and the Wyoming Basin and Great Plains ecoregions. Inset shows the location of Wyoming in the United States. Irregular white shapes are mountainous areas of the Middle and Southern Rockies ecoregions.

transects, 9.65 km long, spaced at 600 m. A pilot and observer scanned from both sides of the plane while traveling at an average groundspeed of 130 km/hr, approximately 60 m above ground. We used a global positioning system (GPS) to record locations and occupancy status of raptor nests within township boundaries, and nests detected while traveling between townships. Detailed methods and abundance results from this survey are included in Olson et al. (2015). Although we recorded all large raptor stick nests, this study included only sites that were occupied by ferruginous hawks when located because we could not assign unoccupied nests to a single raptor species with certainty.

During 2011 and 2012, ferruginous hawk nest sites received ≤3 additional visits during April and May as part of a territory occupancy study (Wallace 2014). Our minimum criteria for occupancy were a single ferruginous hawk in incubating position or a pair associated with a nest structure (Steenhof and Newton 2007). We assessed nest survival and fledgling production at occupied sites during an additional fixed-wing aircraft survey in mid-June. If we could not determine nest status from the aircraft, we made ground visits to accessible sites. We monitored occupancy and estimated spatial covariates within putative breeding territories, defined as 1.5-km radius (7.06-km^2 area) circular buffers around nest sites, based on average breeding territory size of ferruginous hawks (Olendorff 1993). Field work was conducted on public lands that did not require permits for access and on private lands for which we obtained access permissions. Although ferruginous hawks are protected under the Migratory Bird Treaty Act (16 U.S.C. §§ 703–712), no permits were required to conduct our study (including Institutional Animal Care and Use Committee approval) because we did not physically capture or handle animals. We followed guidelines of the Ornithological Council (Fair et al. 2010) to minimize disturbance to nesting ferruginous hawks during aircraft overflights and nest visits.

Response Variables and Covariates

The response variables we evaluated were DSR and fledgling production. We located all nesting attempts early in the breeding period, and therefore, defined initiation of a nesting attempt as the presence of an adult in incubating position on a nest structure. We defined nest survival as continued presence of an adult in incubating or brooding position, or $\geq$1 viable egg or live nestling at the end of each observation interval (Steenhof and Newton 2007). We used data from the literature to estimate length of the nesting period for ferruginous hawks and right-truncated observation intervals to 61 days (Brown et al. 2013), corresponding to an average 32.5-day incubation period, plus 28 days for young to reach approximately 80% of average minimum fledging age (Bechard and Schmutz 1995). We defined DSR as the probability a nest would survive 1 day. We calculated nest success, defined as the probability of $\geq$1 young surviving to 80% of fledging age, as the product of estimated DSR over the 61-day nesting period. We aged nestlings using photographic keys (Moritsch 1985) and defined annual fledgling production as number of young reaching 80% of fledging age (Steenhof and Newton 2007).

Our covariates (Table 1) included prey abundance, vegetative cover, weather, nest substrate, and degree of infrastructure associated with oil and gas development (hereafter anthropogenic infrastructure). Because Wyoming spans portions of several major ecological zones, we included a covariate for ecoregion to account for unknown variation not readily explained by measured factors. We conducted field surveys and used distance sampling methods to generate annual estimates of abundance for mammalian prey species in ferruginous hawk breeding territories during 2010–2012 following Morrison and Kennedy (1989). We used point transects to sample sciurids (Schmutz et al. 2008, Andelt et al. 2009) and line transects for leporids (Wywialowski and Stoddart 1988). We defined a 2-km radius circular buffer around each ferruginous hawk nest site, in which we sampled 6 1-km line transects each with 4 point transects at 333-m intervals; we sampled 1,796 km of line transects in ferruginous hawk home ranges. We used a geographic information system (GIS; ArcGIS Desktop

Table 1. Covariates used in models of daily nest survival (DSR) and fledgling production of ferruginous hawks in Wyoming, USA, 2010–2012. All covariates were estimated for a 1.5-km radius putative ferruginous hawk breeding territory. We averaged daily covariates over observation intervals for models of DSR. For models of fledgling production, we averaged or summed daily covariates over monthly periods, and pooled over months that were strongly correlated. Vegetation data used in models for all years were collected during 2012 and roads data were based on aerial imagery from 2012.

Covariate	Description	Period	Source
Prey abundance			
Squirrel	Abundance of ground squirrels (*Urocitellus* spp.)	Year	Field data
Leporid	Abundance of leporids (*Sylvilagus* spp., *Lepus townsendii*)	Year	
Prairie dog	Abundance of white-tailed prairie dogs (*Cynomys leucurus*)	Year	
Vegetative cover			
Bare	Bare ground (%)	Study	Field data
Shrub	Combined cover of all shrub genera (%)	Study	
Grass	Combined cover of all grass species (%)	Study	
Weather			
Temp min	Minimum daily temperature (°C)	Day	Daly et al. (2008)
Temp max	Maximum daily temperature (°C)	Day	
Precip	Total daily precipitation (mm)	Day	
Storm	Number of days with severe storm events (hail, heavy rain, heavy snow, high wind, thunderstorm wind, winter storms)	Day	National Oceanic and Atmospheric Administration (2006)
Anthropogenic infrastructure			
Well dist	Distance to nearest active oil and gas well pad (m)	Year	Wyoming Oil and Gas Conservation Commission (2013)
Well dist decay	Distance to nearest active oil and gas well pad with 1.5-km decay	Year	
Well pad	Number of active oil and gas well pads	Year	
Oil road	Length of improved roads associated with oil and gas fields (km)	Study	Updated Bureau of Land Management (BLM) data (Wyoming BLM, unpublished data)
Other road	Length of improved roads not associated with oil and gas fields (km)	Study	
Nest substrates			
Substrate	Categorical variable for anthropogenic nest substrates (nest platforms, power poles, and condensation tanks) compared to natural substrates (trees, shrubs, cliffs, rock outcrops, ground)	Year	Field data
Ecoregion			
Ecoregion	Categorical variable for Wyoming Basin compared to Great Plains ecoregion	Study	Chapman et al. (2004)
Time			
Year	Year of study as fixed effect	Year	Field data
Random effect			
Site	Breeding territory as random effect	Study	Field data

Release 10, Environmental Systems Research Institute, Redlands, CA) to place transects randomly within buffers and $\geq$500 m from nest sites to avoid disturbing breeding hawks. Point transects consisted of 5-minute prey observations. Observers ($n = 5$ in 2010, $n = 10$ in 2011 and 2012) conducted 360°-scans of the area surrounding each sample point with binoculars and recorded the species, distance, and azimuth for each sciurid with a range finder and compass. Observers then walked line transects between sample points, recording the species, distance, and azimuth for each leporid detected. We conducted all prey sampling during the ferruginous hawk breeding period in June, and between 0630 and 1030 hours, when prey were active above ground.

We used packages Distance (Distance Version 0.9.3, http://cran.r-project.org/web/packages/Distance, accessed 1 Nov 2014) and Rdistance (Rdistance Version 1.2.1, www.cran.r-project.org/web/packages/Rdistance, accessed 1 Nov 2014) in Program R (R Version 3.1.2, www.r-project.org, accessed 1 Nov 2014) to fit detection functions for line and point transects in each year, and generated annual estimates of abundance for 3 prey groups in each ferruginous hawk territory: ground squirrels (*Urocitellus* spp.), white-tailed prairie dogs (*Cynomys leucurus*), and leporids (*Sylvilagus* spp. and *Lepus townsendii*). We truncated the top 5% of observations to avoid problems with modeling long-tailed distributions (Buckland et al. 2005) and used the Akaike's Information Criterion for small sample sizes (AIC_c; Burnham and Anderson 2002) to select the best-fitting key function for each species, considering half-normal, hazard rate, negative exponential, and uniform. We used the best-fitting detection functions (half-normal key for ground squirrels and prairie dogs, and negative exponential key for leporids) to determine density over all transects and points surveyed in each ferruginous hawk territory, then estimated abundance within territories (see Tables S1 and S2 for summary statistics, available online at www.wildlifejournals.org). For white-tailed prairie dogs, which were frequently detected in small clusters, we modeled the detection function for clusters, and then multiplied estimated cluster densities by average cluster size (Buckland et al. 2005).

We measured vegetative cover along prey transects during the 2012 field season. After completing the prey survey, observers ($n = 10$) retraced their route, sampling vegetation at 60 points located at 100-m intervals along line transects. Observers tossed a 1-m^2 sampling frame to a random location near each point, within which they estimated cover (%) of shrubs by genus, grasses, and bare ground (Wilson 2009). We used these data to define covariates representing territory-level averages of cumulative cover of bare ground, grasses, and shrubs (see Tables S1 and S2 for summary statistics).

We used the PRISM spatial climate model (Daly et al. 2008) and a moving window approach (Potvin et al. 2001) to estimate daily precipitation amount (mm), average daily minimum temperature (°C), and average daily maximum temperature (°C) within ferruginous hawk territories. We used weather records from the National Oceanic and Atmospheric Administration storm events database to define a covariate representing the number of days with $\geq$1 severe storm event (National Oceanic and Atmospheric Administration 2006), based on the approach of Glenn et al. (2011). We included records of hail, heavy rain, heavy snow, high wind, thunderstorm wind, and winter storms from counties and forecast zones in our study area (National Oceanic and Atmospheric Administration 2006). We averaged daily weather values over observation intervals for DSR models (Shaffer 2004; see Table S1 for summary statistics). For fledgling production models, we averaged daily values for temperature and summed daily values for precipitation over monthly periods, corresponding approximately to the stages of ferruginous hawk nesting phenology: territory establishment and egg-laying in April, incubation in May, and brood-rearing in June (Bechard and Schmutz 1995; see Table S2 for summary statistics). We assessed correlation of monthly estimates with Pearson's r and pooled months that were strongly correlated ($r > |0.7|$).

We used available data on locations of oil and gas wells (Wyoming Oil and Gas Conservation Commission 2013) to define covariates representing density of active oil and gas well pads within ferruginous hawk territories, and distances from nest sites to nearest active oil and gas well pads. We also evaluated distance from nest sites to well pads using a 1.5-km decay function (decay function = *exp* (Euclidean distance to feature/–decay distance) to account for greater relative influence of infrastructure closer to nest sites (Carpenter et al. 2010). We updated digital roads data from the BLM by digitizing roads using GIS and aerial photography from the National Agriculture Imagery Program (U.S. Department of Agriculture 2012). We used these data to define covariates representing length (km) of hard-packed, aggregate, or paved roads leading to active oil and gas well pads, including BLM and United States Forest Service (USFS) roads improved for access to oil and gas fields, and length of hard-packed, aggregate, or paved roads not associated with oil and gas fields (see Tables S1 and S2 for summary statistics).

We recorded nest substrates used by ferruginous hawks and mapped alternate nest sites in territories during survey flights (2–4 visits per year) and prey sampling (2 visits per year). We divided substrates into 2 categories for this analysis: anthropogenic (i.e., artificial nest platforms, gas condensation tanks, abandoned windmill platforms, power poles) and natural (i.e., all non-anthropogenic structures, including trees, shrubs, cliffs, rock outcrops, ground).

We used definitions of Chapman et al. (2004) to assign nest sites to the Wyoming Basin or Great Plains ecoregion. We grouped nest sites from the Northwestern Great Plains ecoregion and a single nest that was located in the Western High Plains ecoregion into the Great Plains category because sample sizes were insufficient to model them separately.

Statistical Analyses

We used a 2-step approach to select best-approximating models of DSR and fledgling production as functions of covariates (Olson et al. 2005, Dugger et al. 2011). We first assessed relative importance of covariates within 5 categories representing our ecological hypotheses (i.e., prey abundance, vegetative cover, weather, anthropogenic infrastructure, nest substrate) by fitting univariate linear regressions of covariates on response variables with the base function glm in Program R. Additionally, we evaluated year and ecoregion at this stage. We compared models within each covariate category using AIC$_c$, and retained covariates that ranked within 2 AIC$_c$ of the top model and above the intercept-only model (Dreitz et al. 2012). We calculated pairwise correlations among all covariates and retained the higher-ranked variable from pairs that were strongly correlated. We then used package lme4 (lme4 Version 1.1–7, www.cran.r-project.org/package=lme4, accessed 1 Nov 2014) in Program R to fit generalized linear mixed models for all additive combinations of covariates retained from the univariate stage and including a random effect of site to account for repeated measures of territories among years. We modeled DSR using binomial generalized liner mixed models with a logistic-exposure (LE) link function (Shaffer 2004) to account for the length of time that each nest was under observation, or the exposure period. Observation intervals of unequal length can produce biased estimates of DSR because nesting attempts discovered later in the season effectively have a shorter trial period over which to survive or fail (Johnson 2007). We modeled fledgling production using Poisson generalized linear mixed models. For both analyses, we interpreted models with $\Delta\text{AIC}_c < 2$ and without uninformative parameters (i.e., nested versions of other competitive models with ≥ 1 additional covariate; Arnold 2010) to be competitive best-approximating models. We evaluated standardized covariate point estimates (β), and their 95% confidence intervals (CI) as indicators of the direction and strength of relationships, considering covariate coefficients with CI that did not contain 0 as evidence of strong relationships. We assessed fit of logistic-exposure regression models with the smoothed residual based statistic of Sturdivant et al. (2007) using SAS/IML (SAS System for Windows Version 9.4, SAS Institute, Cary, NC). We assessed fit of Poisson regression models by comparing deviance residuals to model degrees of freedom with χ^2 tests in Program R.

We conducted post hoc analyses to inform interpretation of our findings that DSR and fledgling production varied strongly by nest substrate type. We compared values of continuous covariates between sites with natural and anthropogenic substrates using 2-sample Welch's *t*-tests in Program R. Additionally, we made qualitative assessments of availability of natural substrates in territories where ferruginous hawks nested on anthropogenic structures, and summarized all substrate types used during our study.

RESULTS

From 2010 to 2012, we monitored 109 nesting attempts at 55 ferruginous hawk breeding territories. We included all nesting attempts in models of DSR, which comprised 12 sites with attempts in 1 year, 32 sites with attempts in 2 years, and 11 sites with attempts during all 3 years. These included 48 nesting attempts on anthropogenic substrates and 61 on natural substrates, 98 in the Wyoming Basin and 11 in the Great Plains ecoregion. We monitored each nesting attempt over a single observation interval with

Table 2. Additive models for daily nest survival of ferruginous hawks in Wyoming, USA, 2010–2012. All models included an intercept term and random effect of nest site. Models with $\Delta\text{AIC}_c < 2$ and the statistical null (i.e., intercept-only) model are shown. The dagger (†) indicates the model without uninformative parameters interpreted as the best-approximating model. Provided for each model are number of parameters (*K*), values of the Akaike's Information Criterion for small sample sizes (AIC$_c$), ΔAIC_c, Akaike weight (w_i), and log-likelihood (LL).

Model structure[a]	*K*	AIC$_c$	ΔAIC$_c$	w_i	LL
Substrate + ecoregion	4	140.60	0.00	0.04	−66.11
Substrate + shrub + squirrel	5	140.62	0.01	0.04	−65.02
Substrate + ecoregion + squirrel	5	140.77	0.17	0.04	−65.09
Substrate + squirrel	4	140.91	0.31	0.04	−66.26
Substrate + squirrel + shrub + precip	6	140.93	0.33	0.03	−64.05
Substrate + squirrel + precip	5	140.99	0.39	0.03	−65.20
Grass + squirrel + substrate	5	141.36	0.76	0.03	−65.39
Substrate + shrub	4	141.79	1.18	0.02	−66.70
Substrate + squirrel + shrub + ecoregion	6	142.01	1.41	0.02	−64.59
Substrate + shrub + precip	5	142.07	1.46	0.02	−65.74
Substrate + shrub + ecoregion	5	142.10	1.49	0.02	−65.76
Substrate + squirrel + ecoregion + precip	6	142.10	1.49	0.02	−64.64
Substrate + ecoregion + precip	5	142.12	1.52	0.02	−65.77
Substrate + grass	4	142.13	1.52	0.02	−66.87
Substrate + squirrel + shrub + well pad	6	142.14	1.53	0.02	−64.66
Substrate + precip	4	142.18	1.58	0.02	−66.90
Substrate†	3	142.19	1.59	0.02	−67.98
Substrate + squirrel + well pad	5	142.20	1.59	0.02	−65.81
Substrate + ecoregion + well pad	5	142.30	1.70	0.02	−65.86
Substrate + squirrel + ecoregion + well pad	6	142.33	1.73	0.02	−64.75
Substrate + squirrel + shrub + grass	6	142.48	1.88	0.02	−64.83
Substrate + squirrel + grass + precip	6	142.49	1.88	0.02	−64.83
Intercept-only	2	146.82	6.22	0.00	−71.36

[a] Covariates, estimated within 1.5-km radius breeding territories, were defined as follows: ecoregion, Wyoming Basin compared to Great Plains; grass, cumulative cover of grass; precip, total daily precipitation averaged over exposure periods; shrub, cumulative cover of shrubs; squirrel, abundance of ground squirrels (*Urocitellus* spp.); substrate, anthropogenic compared to natural nest substrates; well pad, number of active oil and gas well pads.

average length 57 days (range = 27–61 days, SE = 0.68). Models of fledgling production included 103 attempts followed until nests failed or young reached 80% of fledging age, which comprised 15 sites with attempts in 1 year, 32 sites with attempts in 2 years, and 8 sites with attempts during all 3 years. These included 44 nesting attempts on anthropogenic substrates and 59 on natural substrates, 92 in the Wyoming Basin, and 11 in the Great Plains ecoregion. Nesting attempts produced an average of 1.47 fledglings (range = 0–4 fledglings, SE = 0.13).

Daily Nest Survival

We evaluated 128 models for DSR consisting of all additive combinations of 7 covariates retained from univariate comparisons (squirrel, shrub, grass, precip, well pad, substrate, ecoregion) and a random effect of nest site. Fixed effects of year on DSR were not supported in univariate models. All 22 models with $\Delta \text{AIC}_c < 2$ included the covariate substrate (Table 2). Therefore, we interpreted the model with substrate as its only fixed effect to be the single best-approximating model and all other models with $\Delta \text{AIC}_c < 2$ as nested versions of that model with additional uninformative covariates (Arnold 2010; Table 2). The best-approximating model suggested DSR was significantly higher for nests on anthropogenic structures compared to natural substrates ($\beta_{\text{substrate}} = 0.67$, 95% CI = 0.17–1.39). This model predicted average DSR of 0.997 (95% CI = 0.994–1.0) for anthropogenic substrates and 0.988 (95% CI = 0.981–0.995) for natural substrates, which translated to an average probability of nest success of 0.83 (95% CI = 0.67–0.98) for anthropogenic substrates and 0.48 (95% CI = 0.26–0.70) for natural substrates over the 61-day nesting period. Non-zero standard deviation for the random effect of site ($\sigma_{\text{site}} = 1.19$) suggested its inclusion in the best-approximating model was warranted, and a goodness-of-fit test (Sturdivant et al. 2007) provided no evidence for lack of fit ($P = 0.77$).

Fledgling Production

We evaluated 256 models for fledgling production consisting of all additive combinations of 8 covariates retained from univariate comparisons (shrub, grass, Jun storm, May precip, Apr precip, well pad, substrate, ecoregion) and a random effect of nest site. Fixed effects of year on fledgling production were not supported in univariate models. We interpreted 2 unique competitive models as best-approximating: the model with substrate as its only fixed-effect, and the model with shrub cover and June storms (Table 3). Additionally, the model including substrate, shrub cover, and June storms was within the 2 ΔAIC_c group, suggesting it was equivalent to both smaller models but did not reduce AIC_c sufficiently to distinguish it as superior (Table 3). We interpreted 12 other models with <2 ΔAIC_c as nested versions of the substrate-only model with additional uninformative covariates (Arnold 2010; Table 3). Similar to results for DSR, the model with substrate suggested fledgling production was significantly greater for nests on anthropogenic structures compared to natural substrates ($\beta_{\text{substrate}} = 0.29$, 95% CI = 0.10–0.50). This model predicted an average of 1.83 fledglings (95% CI = 1.38–2.42 fledglings) from anthropogenic substrates and 1.01 fledglings (95% CI = 0.74–1.38 fledglings) from natural substrates (Fig. 2A). The competitive model with shrub cover and June storms suggested fledgling production had a strong positive relationship to cover of shrubs in breeding territories ($\beta_{\text{shrub}} = 0.28$, 95% CI = 0.08–0.50), and a negative relationship to the number of severe storms during the brood-rearing period in June ($\beta_{\text{Jun storm}} = -0.19$, 95% CI = −0.39 to 0.00; Fig. 2B). The additional model including all 3 parameters supported the same

Table 3. Additive models for fledgling production of ferruginous hawks in Wyoming, USA, 2010–2012. All models included an intercept term and random effect of nest site. Models with $\Delta \text{AIC}_c < 2$ and the statistical null (i.e., intercept-only) model are shown. Daggers (†) indicate models without uninformative parameters interpreted as best-approximating models. Provided for each model are number of parameters (K), values of the Akaike's Information Criterion for small sample sizes (AIC_c), ΔAIC_c, Akaike weight (w_i), and log-likelihood (LL).

Model structure[a]	K	AIC_c	ΔAIC_c	w_i	LL
Substrate + shrub + Jun storm†	5	152.81	0.00	0.04	−71.10
Substrate + shrub	4	152.97	0.16	0.03	−72.28
Substrate + ecoregion	4	153.72	0.91	0.02	−72.66
Substrate + shrub + Apr precip	5	153.76	0.95	0.02	−71.57
Substrate + grass	4	153.83	1.02	0.02	−72.71
Substrate + shrub + ecoregion	5	153.90	1.08	0.02	−71.64
Substrate + shrub + Jun storm + well pad	6	154.03	1.22	0.02	−70.58
Substrate + shrub + well pad	5	154.04	1.23	0.02	−71.71
Substrate + shrub + grass	5	154.34	1.53	0.02	−71.86
Substrate + well pad + ecoregion	5	154.46	1.64	0.02	−71.92
Substrate + shrub + Jun storm + Apr precip	6	154.49	1.68	0.02	−70.81
Substrate + grass + well pad	5	154.69	1.88	0.01	−72.04
Substrate†	3	154.74	1.92	0.01	−74.25
Substrate + Apr precip + ecoregion	5	154.76	1.95	0.01	−72.07
Shrub + Jun storm†	4	154.80	1.98	0.01	−73.19
Intercept-only	2	161.27	8.45	0.00	−78.57

[a] Covariates, estimated within 1.5-km radius breeding territories, were defined as follows: Apr precip, total daily precipitation during April; ecoregion, Wyoming Basin compared to Great Plains; grass, cumulative cover of grass; Jun storm, number of days with severe storm events during June; shrub, cumulative cover of shrubs; substrate, anthropogenic compared to natural nest substrates; well pad, number of active oil and gas well pads.

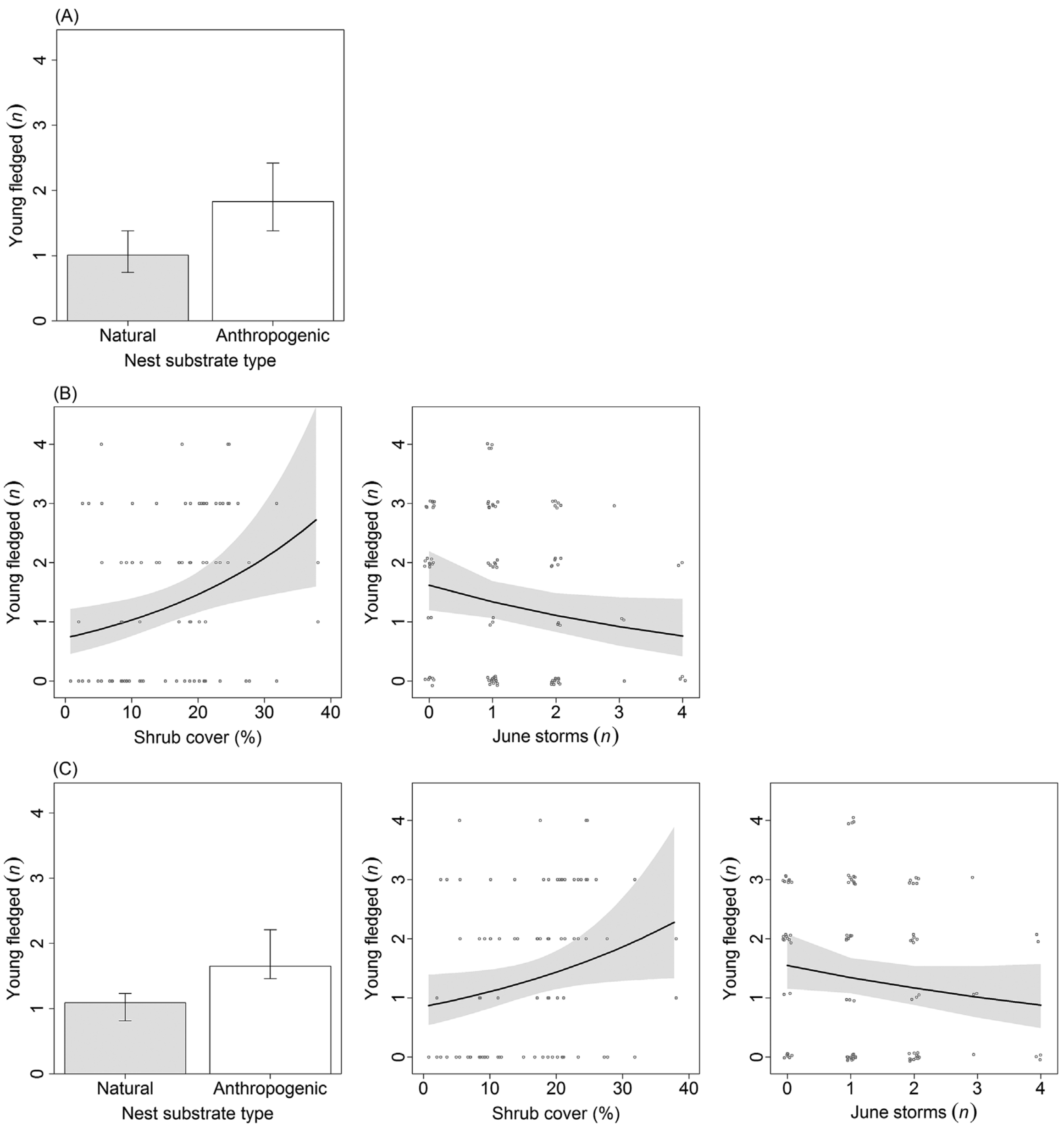

Figure 2. Relationships of covariates to fledgling production of ferruginous hawks in Wyoming, USA, 2010–2012. Depicted are number of young fledged as functions of additive combinations of individual covariates from the 3 best-approximating Poisson generalized linear mixed models with a random effect of nest site and other covariates fixed at mean values: (A) natural versus anthropogenic nest substrate; (B) cover of shrubs within breeding territory and number of severe storms during the June brood-rearing period; and (C) natural versus anthropogenic nest substrate, cover of shrubs within breeding territory, and number of severe storms during the June brood-rearing period. Categorical covariate relationships are illustrated as group means (bars) with 95% confidence intervals (error bars), and numerical covariates as functions (black lines) with 95% confidence intervals (gray bands) and jittered data points (dots).

relationships: greater fledgling production for territories with nests on anthropogenic structures ($\beta_{\mathrm{substrate}} = 0.21$, 95% CI = 0.02–0.83), more shrub cover ($\beta_{\mathrm{shrub}} = 0.21$, 95% CI = 0.01–0.42), and fewer storms during June ($\beta_{\mathrm{Jun\ storm}} = -0.15$, 95% CI = −0.34 to 0.04; Fig. 2C), although the latter relationship was weaker in the 3-parameter model. Non-zero standard deviations for the random effects of site in best-approximating models ($\sigma_{\mathrm{site}} = 0.35$, 0.35, 0.29) suggested their inclusion was appropriate, and Pearson's χ^2 tests provided no evidence of lack of fit ($P = 0.751$, 0.774, 0.588).

Nest Substrates

Of 33 sites with nests on natural substrates, 11 were in cottonwoods (*Populus* spp.), 3 were in junipers (*Juniperus* spp.), 1 in a limber pine (*Pinus flexilis*), 1 in a serviceberry shrub (*Amelanchier* spp.), and 17 on geologic features, including cliffs, rock outcrops, hills, and pinnacles. Of 22 sites on anthropogenic substrates, 17 were on artificial nest platforms designed for ferruginous hawks, 2 on derelict wooden windmill platforms, 1 on a power pole, 1 on an abandoned tank in a former oil field, and 1 on an active natural gas condensation tank. Anthropogenic nest structures used by ferruginous hawks occurred mostly in flat, open terrain that lacked other elevated substrates: only 2 territories with anthropogenic substrates contained $\geq$1 tree, and only 4 territories had alternate nest sites on other natural substrates (i.e., geologic features). Most anthropogenic nesting substrates used by ferruginous hawks were not located in energy developments: only 8 were in active oil and gas fields (including 1 site <1 km from the edge of an active coal strip mine, and 1 nest on an active natural gas condensation tank). Two sites were <500 m from Interstate-80, and 2 sites were $\leq$3 km from wind turbines. Remaining sites with anthropogenic substrates were in remote, relatively unmodified areas, including 10 artificial nest platforms installed to improve habitat for ferruginous hawks in a 700-km^2 area of Wyoming's central Great Divide Basin (Tigner et al. 1996, Neal et al. 2010).

Post hoc *t*-tests revealed no significant differences between territories with natural and anthropogenic substrates for values of covariates representing prey abundance, vegetation, weather, and anthropogenic infrastructure. This included no significant differences by substrate among covariates from competitive models for fledgling production: shrub cover ($P = 0.084$, $\bar{x}_{\text{natural}} = 14.23$, $\bar{x}_{\text{anthropogenic}} = 18.15$) and average number of days with severe storms in June ($P = 0.946$, $\bar{x}_{\text{natural}} = 1.27$, $\bar{x}_{\text{anthropogenic}} = 1.27$). Although territories with anthropogenic substrates had higher average density of active oil and gas well pads (0.56 well pads/km^2, range = 0–2.55 well pads/km^2, SE = 0.19) than territories with natural substrates (0.36 well pads/km^2, range = 0–2.55 well pads/km^2, SE = 0.13), this difference was also not significant ($P = 0.392$).

DISCUSSION

Average DSR of ferruginous hawks during our study was high (>0.99 for anthropogenic substrates and >0.98 for natural substrates) and comparable to estimates for other birds of prey: $\geq$0.96 for Aplomado falcon (*Falco femoralis septentrionalis*; Brown and Collopy 2012), $\geq$0.99 for barn owl (*Tyto alba*; Martin et al. 2010), and 0.99 for grasshopper buzzard (*Butastur rufipennis*; Buij et al. 2013). Average probability of success for ferruginous hawk nests on anthropogenic substrates (0.83, 95% CI = 0.67–0.98) was higher than estimates for all substrate types from other studies that accounted for length of observation periods (0.59, Van Horn 1993; 0.40–0.57, Lehman et al. 1998), whereas nesting success on natural substrates was slightly lower (0.48, 95% CI = 0.26–0.70). Average number of fledglings produced per nesting attempt during our study (1.47 fledglings, range = 0–4, SE = 0.13) was within the range of variation recorded for this species (Table 4). Our estimate of average number of young fledged from anthropogenic structures (1.83 fledglings, 95% CI = 1.38–2.42) was below the lowest annual average reported by Tigner et al. (1996) for artificial nest platforms in Wyoming during 1988–1993 ($\bar{x} = 2.46$, range = 1.91–3.45). Although these results suggest fledgling production on artificial nest platforms may have been depressed during our study, it is unclear whether productivity declined over time, or this relationship resulted from differences in methodology.

Table 4. Estimates of average annual fledgling production for ferruginous hawks published since the comprehensive summary of Olendorff (1993). Shown are mean and range of average annual number of fledglings per nesting attempt, state or province where study took place, and source.

Mean	Range	Location	Source
1.77		Montana	Restani (1991)
2.30[a]	1.50–3.27	Idaho	Steenhof et al. (1993)
1.15	0.80–1.50	Montana	Van Horn (1993)
0.96	0.92–1.00	Montana	Zelenak and Rotella (1997)
2.00	1.70–2.30	Utah	Ward (2001)
1.73	1.30–2.00	New Mexico	Cartron et al. (2002)
2.82	2.24–3.38	Saskatchewan	Houston and Zazelenchuk (2005)
1.32		Utah	Keough (2006)
2.71	2.08–3.38	Alberta	Schmutz et al. (2008)
1.94	1.50–2.60	Oklahoma	Wiggins et al. (2014)
1.47	1.38–1.69	Wyoming	This study

[a] Included non-breeding pairs.

Buteo hawks and other raptors partition habitat by nest substrate and land cover type (Bechard et al. 1990, McConnell et al. 2008, Kennedy et al. 2014) in response to limited availability of nest sites in non-forested habitats (Restani 1991, Janes 1994). The flexibility of ferruginous hawks to nest on anthropogenic structures (Gilmer and Stewart 1983, Bechard and Schmutz 1995) may, thus, be an adaptation to reduce inter-specific competition for nest substrates. Although other raptors and corvids also nest on anthropogenic structures, Steenhof et al. (1993) reported this behavior was only associated with increased reproductive success for ferruginous hawks, whereas nesting on transmission towers did not increase nest success for red-tailed hawks (*Buteo jamaicensis*), golden eagles (*Aquila chrysaetos*), or common ravens (*Corvus corax*). Use of artificial nest structures may also indirectly reduce risk of avian nest predation by species including golden eagles, which are known to predate ferruginous hawk nestlings (Keough 2006, Neal et al. 2010). Although we did not formally test this hypothesis, we speculate ferruginous hawks may reduce their risk of nest predation by selecting sites on anthropogenic substrates in open, basin-level habitats that tend to be farther from the rough, upland nesting habitat of golden eagles (MacLaren et al. 1988, Kochert et al. 2002, Tack and Fedy 2015). Nests on anthropogenic structures may also be less accessible to ground-based mammalian predators than those on trees and some rock outcrops (Schmutz et al. 1984, Roth and Marzluff 1989, Neal et al. 2010). The absence of other available nesting substrates in most territories at which ferruginous hawks used anthropogenic structures was consistent with previous research suggesting suitability of breeding habitat for this species was improved by addition of low-density infrastructure, including platforms designed for nesting raptors (Tigner et al. 1996, Neal et al. 2010, Wallace 2014), power transmission support structures (Gilmer and Stewart 1983, Steenhof et al. 1993), and gas condensation tanks (Keough and Conover 2012). It was not clear whether colonization of anthropogenic substrates resulted from local shifts in distribution of ferruginous hawks, as suggested by some authors (Gilmer and Stewart 1983, Tigner et al. 1996, Neal et al. 2010), or availability of anthropogenic structures increased regional population density (Schmutz et al. 1984, Steenhof et al. 1993).

Contrary to our prediction, breeding territories with relatively greater shrub cover produced more young. In our study area, the sagebrush-steppe habitats of the Wyoming Basin have greater shrub cover than the grasslands of the Great Plains (Knight 1996); however, models with shrub cover out-performed models with effects of ecoregion, suggesting the positive relationship of fledgling production with shrub cover could not be explained by ecoregion alone. Shrub cover was also not correlated with abundance of ground squirrels, prairie dogs, or leporids, which indicated vegetation cover was not a proxy for prey habitat. Greater amounts of shrub cover may have been associated with prey species not sampled during our study (e.g., black-tailed prairie dogs, *Cynomys ludovicianus*; and pocket gophers, *Thomomys* spp.), or reduced predation risk and inter-specific competition in lowland areas; however, further research is necessary to clarify the mechanisms underlying the positive relationship between fledgling production and shrub cover.

Fewer young fledged from ferruginous hawk territories that experienced more days with severe storms during the June brood-rearing period. This result supported our prediction that severe spring weather would negatively affect productivity of ferruginous hawks in a manner consistent with other raptors (Sergio 2003, Kostrzewa and Kostrzewa 2008). Although ferruginous hawks evolved with the variable spring weather of the Great Plains and Intermountain West, storms are predicted to become more frequent and intense as a result of anthropogenic climate change (Wuebbles et al. 2014). These shifts in regional weather patterns are expected to have negative effects on grassland birds (Skagen and Yackel Adams 2012), and our results suggest they could negatively affect productivity of ferruginous hawks. Furthermore, the exposed nest placement characteristic of ferruginous hawks (Bechard and Schmutz 1995) may make them especially susceptible to nest failure and destruction from hail and wind (Lokemoen and Duebbert 1976, Gilmer and Stewart 1983, Steenhof et al. 1993). The effect of storms on fledgling production was weaker than other relationships in our study, possibly because available severe-storm data were spatially coarse and we had to average daily weather data over long intervals given frequency of nest checks.

Contrary to our predictions, nest success and productivity of ferruginous hawks were not related to abundance of ground squirrels, white-tailed prairie dogs, or leporids. Previous studies of ferruginous hawks found positive correlations of fledgling production with abundance of jackrabbits (Woffinden and Murphy 1989, Keough 2006), density of ferruginous hawks with abundance of ground squirrels (Schmutz et al. 2008), and nest success with road and agricultural edges used by ground squirrels (Zelenak and Rotella 1997). However, studies of other raptors reported reproduction was not limited by food availability in all years (Ward and Kennedy 1996, Dewey and Kennedy 2001). In light of strong evidence for a positive relationship of territory occupancy with ground squirrel abundance in our study area during 2 of 3 years of this study (Wallace 2014), our results suggest prey abundance influenced the probability that ferruginous hawks initiated nesting but did not influence nest success or fledgling production.

Our results provided no evidence that breeding performance was influenced by density of roads and oil and gas well pads, or distance to well pads. Previous studies on effects of roads and well pads on ferruginous hawks are equivocal: some document positive relationships of productivity with certain types of roads (Zelenak and Rotella 1997) and occupancy with roads (Neal et al. 2010, Wallace 2014) and well pads (Keough and Conover 2012), whereas others report negative relationships of productivity with well pads (Harmata 1991, Keough 2006), and no apparent response of occupancy (Wallace 2014) or breeding success (Van Horn 1993) to well pads. Although we accounted for a wider range of natural and anthropogenic factors than earlier studies, our ability to assess potential disturbance from roads and well pads may have been limited because of the low density of energy infrastructure at occupied nest sites. Average density of active oil and gas well pads in occupied territories with ≥ 1 pad considered in this study was considerably lower (1.34 well pads/km^2) than some current and proposed developments in Wyoming (e.g., 32-ha spacing = 3.08 well pads/km^2; 16-ha spacing = 6.16 well pads/km^2).

Our study was observational and conducted after construction of anthropogenic structures and energy developments, and, thus, does not address effects these factors may have had on historical density or distribution of ferruginous hawks. Therefore, nesting sites used by ferruginous hawks in developed areas possibly had characteristics that minimized potential negative impacts of infrastructure or were occupied by individuals tolerant of disturbance. However, our study design is common because many landscape-level development projects are approved and implemented by regulatory agencies before pre-treatment data can be collected (Kennedy 1980, Northrup and Wittemyer 2012, Allred et al. 2015). Until this process changes, the ability of post-impact, observational studies to inform management is limited—even for studies conducted at large spatial scales with probabilistic sampling.

Although our results suggest some types of anthropogenic infrastructure are associated with increased reproductive success for ferruginous hawks, a complete assessment of effects of infrastructure on population viability for this species would require accounting for its known negative effects on survival of adult and juvenile raptors, including fatality from electrocution (Lehman et al. 2007) and collision (Erickson et al. 2005). We also do not understand how anthropogenic structures could alter regional distributions or nest-selection behavior of ferruginous hawks over the long-term. We suggest future mechanistic studies of ferruginous hawk ecology could be complemented by rigorous long-term population monitoring using probabilistic sampling and methods to account for imperfect detection. Risk maps based on monitoring data could then be used to prioritize conservation of frequently occupied and highly productive territories (Tack and Fedy 2015), and siting of energy developments in less suitable habitat where artificial nest structures could be used to mitigate impacts.

MANAGEMENT IMPLICATIONS

Our results suggest artificial nest platforms are a primary factor influencing nest survival and productivity of ferruginous hawks in Wyoming. Artificial platforms and other anthropogenic structures (i.e., gas condensation tanks, abandoned windmill platforms, power poles) increased nest survival and productivity given the density of human disturbance present in the study area. Anthropogenic nesting substrates appear not to be ecological traps and have potential use in mitigation; however, effectiveness of artificial nest platforms as a management tool should be evaluated experimentally with pre-treatment data incorporated into sampling designs. Although ferruginous hawks nested in some areas with very little vegetative cover, they produced more than average number of young in areas with $\geq$20% shrub cover. Efforts used to maintain shrub cover for other shrub-dependent species of conservation concern, such as the greater sage-grouse (*Centrocercus urophasianus*; Connelly et al. 2000), may, therefore, also sustain or increase productivity of ferruginous hawks. The negative impact of severe spring storms on fledgling production illustrates the importance of including future climate and weather scenarios in management plans for ferruginous hawks, as storms are predicted to increase in frequency and intensity as the result of climate change. Finally, we view our study as providing an opportunity for wildlife and land managers to evaluate impacts of future development. We strongly recommend that our methods and results be used as baseline data for monitoring on an annual or biannual schedule, and the intensive survey detailed by Olson et al. (2015) be conducted on a 10-year schedule and results evaluated with the updated covariates.

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