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FACTORS INFLUENCING REPRODUCTIVE SUCCESS OF FERRUGINOUS HAWKS IN THE UINTAH BASIN, UTAH

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ABSTRACT.—We examined factors that potentially influenced reproductive success in Ferruginous Hawks (*Buteo regalis*) in the Uintah Basin, Utah, and determined whether oil and gas well development was one of those factors. For three breeding seasons (2002–2004), we measured the number of nestlings, fledglings, and dispersed young that were produced by pairs of Ferruginous Hawks nesting within 2365 km² managed by the Bureau of Land Management. We hypothesized that reproductive success would be influenced by nesting substrate, abundance of prey, distance to the closest occupied raptor nest, and distance to the closest active well. Although the Uintah Basin experienced a drought during our entire study, reproductive success was within the range of estimates reported in other studies in the Intermountain West. Each nesting pair produced an average of 1.9 nestlings, 1.3 fledglings, and 0.9 dispersed young. During our study, 17 nestlings and 14 fledglings died; 55% were due to avian predators, 16% to mammalian predators, 10% to unknown predators, 16% to natural causes, and 3% to unknown causes. Avian depredation may have resulted from increased competition among avian predators for scarce prey resources, or from increased use of juvenile Ferruginous Hawks as an alternative prey source by Golden Eagles (*Aquila chrysaetos*) in years of low lagomorph abundance. Our results suggest that the level of oil development that occurred during this study did not have an adverse effect on Ferruginous Hawk reproduction; the effect of a higher level of oil development was beyond the scope of this study.

KEY WORDS: *Ferruginous Hawk*; *Buteo regalis*; brood survival; dispersed young; fledgling survival; gas development; oil development; reproductive success.

FACTORES QUE INFLUYEN EN EL ÉXITO REPRODUCTOR DE *BUTEO REGALIS* EN LA CUENCA DE UINTAH, UTAH

RESUMEN.—Examinamos los factores que influyen potencialmente sobre el éxito reproductor de *Buteo regalis* en la Cuenca de Uintah, Utah y determinamos si el desarrollo de pozos de extracción de petróleo y gas fue uno de estos factores. Durante tres épocas reproductivas (2002–2004) cuantificamos el número de pollos en el nido, número de pollos volanderos y el número de jóvenes dispersantes criados por parejas de *B. regalis* que nidificaron en el interior de los 2365 km² administrados por el Departamento de Gestión del Suelo. Planteamos la hipótesis de que el éxito reproductor podría estar influido por el sustrato del nido, la abundancia de presas, la distancia al nido ocupado de aves rapaces más cercano y la distancia al pozo activo más cercano. Aunque la Cuenca de Uintah experimentó una sequía durante todo el tiempo que duró nuestro estudio, el éxito reproductor estuvo dentro del rango estimado encontrado por otros estudios en el Oeste Intermontano. Cada pareja reproductora sacó adelante un promedio de 1.9 pollos en nido, 1.3 pollos volanderos y 0.9 jóvenes dispersantes. Durante nuestro estudio, 17 pollos en nido y 14 pollos volanderos murieron, 55% fue debido a depredación por aves, 16% a depredación por mamíferos, 10% a depredadores desconocidos, 16% a causas naturales y 3% a causas desconocidas. La depredación por parte de aves puede haber sido el resultado de la competencia creciente entre aves depredadoras por la escasez de presas o debido al incremento en el uso de individuos juveniles de *B. regalis* como fuente alternativa de presas por parte de *Aquila chrysaetos* en años de baja abundancia de lagomorfos. Nuestros resultados sugieren que el nivel de desarrollo de la extracción de petróleo alcanzado durante nuestro estudio no tuvo un efecto adverso en la reproducción de *B. regalis*. El efecto de un mayor nivel de desarrollo petrolífero estuvo más allá del alcance de este estudio.

[Traducción del equipo editorial]

The reproductive success of Ferruginous Hawks (*Buteo regalis*) varies based on prey abundance, competition for space with other breeding raptors,

mammalian and avian depredation, and human disturbance. Ferruginous Hawk nesting density and nesting success are closely related to prey abundance and availability (Smith et al. 1981, White and Thurow 1985, Stalmaster 1988, Woffinden and

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Murphy 1989, Zelenak and Rotella 1997, Ward 2001, Dechant et al. 2003). Ferruginous Hawks primarily prey on mammals including ground squirrels (*Spermophilus* spp.), pocket gophers (*Thomomys* spp.), prairie dogs (*Cynomys* spp.), and jackrabbits (*Lepus* spp.), although birds, reptiles, and insects are taken (Smith and Murphy 1978, Bechard and Schmutz 1995, Dechant et al. 2003, Keeley 2009).

Schmutz (1989) reported that intraspecific and interspecific competition for space occurs between Ferruginous Hawk nesting pairs and other breeding raptor species. When Ferruginous Hawks, Red-tailed Hawks (*Buteo jamaicensis*), and Swainson's Hawks (*Buteo swainsoni*) nest in close proximity, their reproductive success declines (Schmutz et al. 1980). Zelenak and Rotella (1997) found that Ferruginous Hawks nesting farther from nests of other raptors produced more young than those nesting closer to other raptors, suggesting reproductive success was negatively influenced by intraspecific and interspecific competition.

Golden Eagles (*Aquila chrysaetos*), Prairie Falcons (*Falco mexicanus*), Great Horned Owls (*Bubo virginianus*), coyotes (*Canis latrans*), red foxes (*Vulpes vulpes*), and American badgers (*Taxidea taxus*) are predators of Ferruginous Hawk eggs and nestlings (Van Horn 1993, Bechard and Schmutz 1995). Different nesting substrates provide varying degrees of protection from predation (Roth and Marzluff 1989). In the Uintah Basin, historical nest sites occur on the ground, cliff ledges, Utah juniper trees (*Juniperus osteosperma*), rock pinnacles, and human-made structures. It is possible that elevated substrates provide more protection from mammalian predators than ground nests.

Lokemoen and Duebbert (1976) and Ward (2001) reported avian predation on Ferruginous Hawk nests. In Utah's West Desert, Ward (2001) found that avian predators killed some adult Ferruginous Hawks and were the primary cause of juvenile mortality. The threat of avian depredation may increase if Ferruginous Hawks nest in close proximity to other occupied raptor nests or during years of low prey abundance when juvenile hawks may serve as an alternative food source (Ward 2001). The raptor species most likely to depredate Ferruginous Hawk nests in the Uintah Basin include Golden Eagles, Great Horned Owls, and other Ferruginous Hawks.

Ferruginous Hawks generally locate their nests away from human disturbance (Schmutz 1984, Roth and Marzluff 1989). Nests in remote locations usually have greater reproductive success than nests more exposed to human activities and develop-

ments (Dechant et al. 2003). However, tolerance to human disturbance is variable and may be influenced by prey availability, nesting substrate, timing of disturbance, and individual behavior (Gilmer and Stewart 1983, White and Thurow 1985, Dechant et al. 2003, Keeley 2009). The primary effects of human disturbance include decreased reproductive performance, direct mortality, and habitat alteration that decreases prey abundance and/or nest site availability (Smith and Murphy 1978, Gilmer and Stewart 1983, White and Thurow 1985, Olendorff 1993). Ferruginous Hawks are especially sensitive to human disturbance during nest-site selection and incubation; even mild disturbance during these periods can lead to nest abandonment (Smith and Murphy 1978, Gilmer and Stewart 1983, White and Thurow 1985, Bechard et al. 1990, Leslie 1992, Olendorff 1993, Dechant et al. 2003). Disturbed nests may fledge fewer young and are often not reoccupied the following year (White and Thurow 1985).

Over the last two decades, the Uintah Basin in eastern Utah has experienced substantial oil and gas development and a concomitant decline in breeding population of Ferruginous Hawks (Keough 2006). Oil and gas well developments result in habitat alteration, road construction, and increased recreational use (Olendorff 1993). It is important to understand the potential effects of well development on Ferruginous Hawk reproductive success in the Uintah Basin to protect breeding hawks.

To learn more about Ferruginous Hawk nesting ecology in the Uintah Basin, we examined which factors may influence reproductive success. We predicted *a priori* that Ferruginous Hawk nests would be more successful if located on elevated substrates (e.g., juniper tree, rock pinnacle, human-made structure), in areas with more prey, and far from other occupied raptor nests or active wells. Thus, nine variables were of interest: (1) nesting substrate, (2) abundance of prairie dogs, (3) number of lagomorphs seen while walking line-transects, (4) number of lagomorphs spotted while driving road-transsects, (5) distance to the nearest occupied raptor nest, (6) number of raptors seen while conducting prey surveys (e.g., raptor activity), (7) number of other occupied raptor nests, (8) distance to closest active well, and (9) number of active wells.

METHODS

Study Area. Our study was conducted on land managed by the Bureau of Land Management

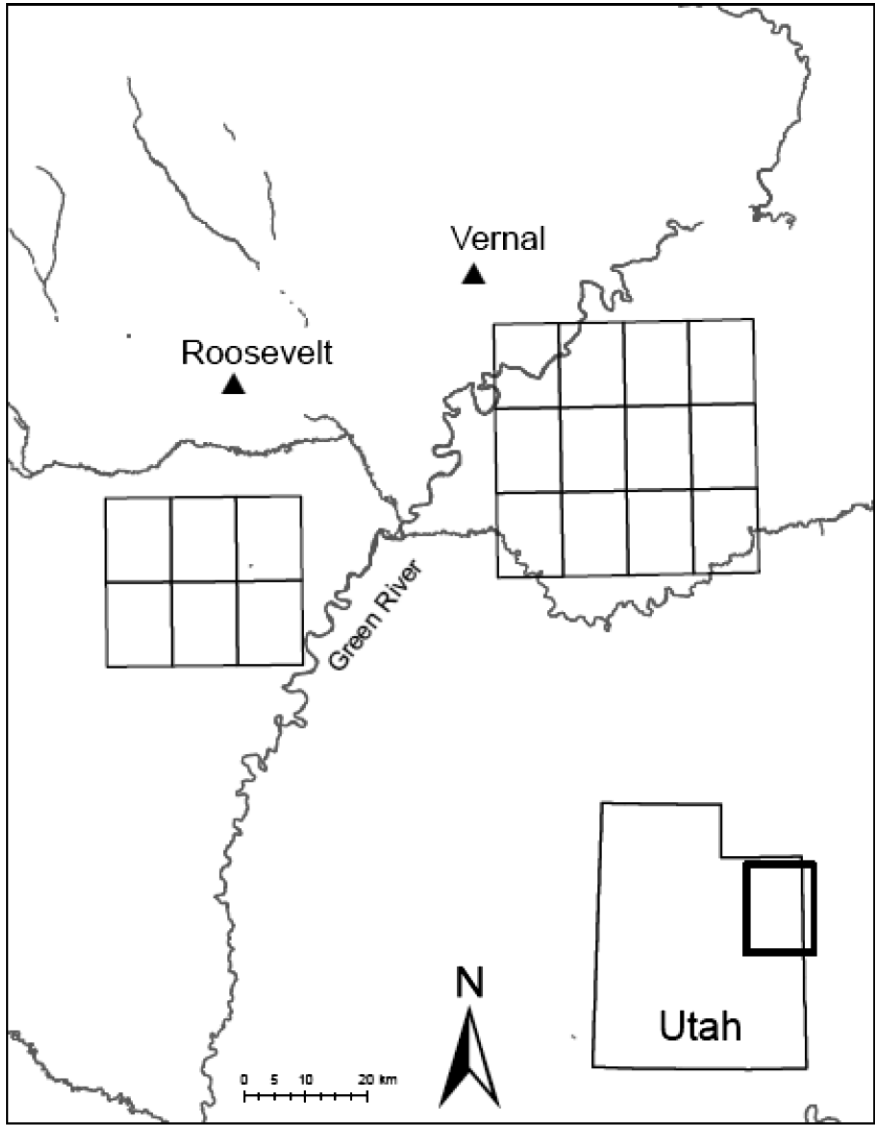


Figure 1. Our 2365-km² study area within Utah's Uintah Basin included 16 7.5-minute quadrangle maps which are shown as rectangles on the map (each rectangle is 10.5 km wide and 12.4 km long). These maps included: Crow Knoll, Myton SW, Myton SE, Pariette Draw SW, Wilkin Ridge, Red Wash SE, Red Wash SW, Bonanza, Walsh Knolls, Dinosaur, Dinosaur NW, Red Wash, Red Wash NW, Cliff Ridge, Jensen, and Rasmussen Hollow.

(BLM) Vernal Field Office in the Uintah Basin located in eastern Utah. The approximately 2365-km² area included 16 7.5-min quadrangle maps (Fig. 1). The 28 205-km² Uintah Basin lies at about 1500 masl and is part of both the Colorado Plateau and the cold desert biome. The climate was semiarid with low humidity. During the nesting season, typical

rainfall was 1.3 to 2.2 cm of rainfall/mo, with average temperatures of 8° to 21°C (http://www.desertusa.com/Cities/ut/ut_vernal.html). The study area is divided into two vegetation zones by the Green River due to regional differences in precipitation, with shrub-grass on the west side and a mixture of shrub-grass and Utah juniper on the east side. Five

of the 16 7.5-min quadrangle maps occur west of the Green River, and the remaining 11 occur east of the Green River.

Identifying Occupied Nest Sites. Ferruginous Hawks demonstrate breeding site fidelity, often re-occupying historical nesting territories and nest sites (Smith and Murphy 1978). Thus, our surveys for breeding activity largely focused on visiting areas with previously occupied nest sites. Between March and April of 2003 and 2004, we searched for occupied Ferruginous Hawk nests by visiting all historical Ferruginous Hawk nest sites that were listed as occupied between 1998 and 2002 by the BLM Vernal Field Office or by R.C. Etchberger at the Uintah Basin Campus of Utah State University. We also visited all Ferruginous Hawk nest sites we recorded as occupied during previous field seasons. In addition, the BLM Vernal Field Office and R.C. Etchberger provided access to an ArcView database that listed all known historical raptor nest sites within our study area. Each year, we randomly selected and visited 50 of these historical Ferruginous Hawk nest sites from this database. Because vegetation differs on the east and west sides of the Green River, we selected historical nest sites so they were proportionally distributed on both sides of the Green River. Between 1998 and 2000, approximately 80% of Ferruginous Hawks nested east of the Green River. Thus, historical nest sites were selected such that approximately 40 (80%) occurred on the east side of the study area and 10 (20%) occurred on the west side of the study area. All selected nests were visited twice; once in March and once in April.

Because nesting pairs are sensitive to disturbance during nest-site selection, courtship, and incubation (Keeley and Bechard 2011), we assessed territory occupancy after 30 April and from the vehicle at a minimum distance of >500 m using a spotting scope for >30 min. Because most nests were not visible at >500 m, we did not assess territory occupancy by directly observing nesting activity. Rather, observations of adult activity in the area were used to assess territory occupancy. If a Ferruginous Hawk was observed during one of the two ground visits, we recorded the territory as a potentially occupied nesting territory.

Additionally, we surveyed for occupied nest sites by flying transects for >20 hr over the study area during late May and early June using a fixed-wing aircraft following the method of Ayers and Anderson (1999). During these flights, we checked historical Ferruginous Hawk nest sites and also flew

randomly selected transect coordinates to search for unknown nests. To maximize detection of nests and minimize potential disturbance to nesting Ferruginous Hawks, transects were flown at an average speed of 145 km/hr and a height of 60 m. A single-pass technique was used in which the aircraft did not deviate from transects unless observers needed to confirm nest observations (Ayers and Anderson 1999). We recorded nests as occurring within potentially occupied nesting territories if we observed a Ferruginous Hawk near or on a nest during flights.

Nests were classified as occupied and occurring within an occupied nesting territory if we observed: (1) an adult on a nest or demonstrating defense behavior, (2) a pair of adults in the area consistently, or (3) eggs or hatchlings in a nest. Defense behavior includes stooping or circling the nest site or the observer and vocalizing. We defined "nesting pair" as a pair of birds having an occupied nest in a given year. Hereafter, the nests of Ferruginous Hawks will be referred to as just "nests"; the nests of other species will be identified as to species or species group (e.g., Golden Eagle nest or raptor nests).

Assessing Reproductive Success. Previous studies have measured reproductive success of Ferruginous Hawks by counting the number of eggs hatched and the number of hatchlings that successfully fledged (Lokemoen and Duebbert 1976, Smith and Murphy 1978, White and Thurow 1985, Stalmaster 1988, Roth and Marzluff 1989, Zelenak and Rotella 1997). However, only a few studies have monitored Ferruginous Hawk offspring past the fledging stage through to dispersal in late summer and early fall from the natal area (Blair and Schitoskey 1982, Konrad and Gilmer 1986, Zelenak et al. 1997). We did not measure the number of eggs hatched to minimize the risk of nest abandonment, but instead counted the number of nestlings, fledglings, and dispersed young (e.g., the number of fledglings that successfully dispersed) produced by each nesting pair of Ferruginous Hawks.

During mid-June, when downy young should be visible in nests, we revisited all occupied nest sites and counted the number of nestlings. We observed them from a distance of >250 m and used binoculars and spotting scopes to confirm whether nests were occupied and the number of nestlings present. When nestlings were 21–30 d old, they were captured by hand and fitted with tarsal-mounted transmitters. This age was chosen to reduce the chance that nestlings might jump from the nest to avoid

Table 1. Abbreviations for the nine potential explanatory variables used in regression tree analysis to differentiate: (1) occupied nests that produced zero, one, two, three, or four nestlings; (2) occupied nests that produced zero, one, two, three, or four fledglings; and (3) occupied nests that produced zero, one, two, or three dispersed young. Occupied nests were located within the Uintah Basin, eastern Utah, during three breeding seasons (2002–2004).

EXPLANATORY VARIABLE	ABBREVIATION
Nesting substrate	NEST_SUB = LEDG, PINN, JUNI, or MAN
Total number of white-tailed prairie dogs seen during line-transects	NO_PDLINT
Total number of lagomorphs seen during line-transects	NO_LGLINT
Total number of lagomorphs seen during road-transects	NO_LGRDT
Distance in m to closest other occupied raptor nest	DIS_NRRAP
Total number of raptors seen while conducting line-transects	NO_RAPLNT
Number of other occupied raptor nests within 1-, 1.5-, 2-, 2.5-, 3-, 3.5-, and 4-km radii of each site	CNTR_4000, CNTR_3500, CNTR_3000, CNTR_2500, CNTR_2000, CNTR_1500, and CNTR_1000
Distance in m to closest active well	DIS_NRWEL
Number of active wells within 1-, 1.5-, 2-, 2.5-, 3-, 3.5-, and 4-km radii of each site	CNTW_4000, CNTW_3500, CNTW_3000, CNTW_2500, CNTW_2000, CNTW_1500, and CNTW_1000

capture and subsequently injure themselves. In addition, by the time nestlings are ca. 21 d old, their tarsus width is similar to an adult's (J. Ward, The Nature Conservancy, pers. comm.). Capture and handling protocols complied with the standards of the Institutional Animal Care and Use Committee (IACUC) at Utah State University (IACUC Approval #1034). We did not place bands or radio-transmitters on nesting adults to minimize the risk of nest abandonment and reduced nest success, and to avoid confounding the effects of capture activities and oil and gas well development on reproductive success.

Using radiotelemetry, we monitored each nestling and juvenile every 3–5 d at a distance of >250 m until the bird died or dispersed. Following 8 hr of inactivity, the tarsal-mounted transmitters emitted a mortality signal. Upon receiving a mortality signal, we located and collected the deceased juvenile. Using field observations and necropsies, we determined whether juveniles were killed by mammalian or avian predators, died of other natural causes (e.g., injury, starvation, disease), or died of unknown causes. Predator type was differentiated based on location of carcass remains (i.e., tree, ground, originating nest, other hawk or eagle nest), presence of mammalian tracks, measurement of puncture wounds from talons or teeth, and whether a carcass was dismembered. Juveniles killed by avian predators often were not dismembered, had broken necks and puncture wounds from talons, and were found in their originating nests.

Potential Factors Influencing Reproductive Success. We investigated the influence of the following

variables on reproductive success: (1) nesting substrate, (2) abundance of prairie dogs, (3) number of lagomorphs seen while walking line-transects, (4) number of lagomorphs spotted while driving road-transects, (5) distance to the nearest occupied raptor nest, (6) number of raptors seen while conducting prey surveys (e.g., raptor activity), (7) number of other occupied raptor nests, (8) distance to closest active well, and (9) number of active wells. We classified the substrate of occupied nests into four categories: cliff ledge (LEDG), rock pinnacle (PINN), juniper tree (JUNI), and human-made structures (MAN; Table 1). To ensure that we included the entire breeding home range for nesting Ferruginous Hawk pairs in the assessment of prey resources and competitive interactions, we collected data within a circle centered at the nest site and extending out for 4 km (50.2 km² area). We used such a large area because it was larger than the average estimate of home-range size for breeding Ferruginous Hawks (35 km²) based on the published reports of 6, 7, and 90 km² by Smith and Murphy (1978), Olendorff (1993), and Leary et al. (1998), respectively.

We used a line-transect sampling method that estimated prey numbers by focusing on prey observed aboveground. To obtain a relative measure of prey abundance, we used a consistent sampling effort for all surveys. To do so, we centered around each nest a 2-km by 2-km square, with a 2-km line-transect arranged along each side (8-km total) with starting points at the top-right, top-left, bottom-right, and bottom-left corners. This arrangement placed the center of each line-transect 1.0 km from the nest

Table 2. Predicted and observed associations between the nine potential explanatory variables and Ferruginous Hawk nests producing more young. Predicted associations were based on research hypotheses developed from the literature. Observed associations were based on the values of explanatory variables included in at least one of the three “best” regression trees differentiating: (1) occupied nests that produced zero, one, two, three, or four nestlings; (2) occupied nests that produced zero, one, two, three, or four fledglings; and (3) occupied nests that produced zero, one, two, or three dispersed young. Occupied nests were located within the Uintah Basin, eastern Utah, during three breeding seasons (2002–2004).

PREDICTED ASSOCIATION	OBSERVED ASSOCIATION
NEST_SUB = JUNI, PINN, or MAN	NEST_SUB = no association
NO_PDLINT = relatively high abundance	NO_PDLINT = no association
NO_LGLINT= relatively high abundance	NO_LGLINT = relatively higher abundance
NO_LGRDT= relatively high abundance	NO_LGRDT = no association
DIS_NRRAP = relatively large distance to nearest other occupied raptor nest	DIS_NRRAP = relatively small distance to nearest other occupied raptor nest
NO_RAPLNT = relatively low number of other raptors seen	NO_RAPLNT = relatively higher number of other raptors seen
CNTR = relatively low number of other occupied raptor nests	CNTR = no association
DIS_NRWEL = relatively large distance to nearest active well	DIS_NRWEL = no association
CNTW = relatively low number of active wells	CNTW = relatively higher number of active wells

and the corners 1.1 km from the nest. We did this to minimize disturbance to nesting pairs. We walked clockwise along each line-transect between 0700 and 1300 H and recorded the number of white-tailed prairie dogs (*Cynomys leucurus*), desert cottontails (*Sylvilagus audubonii*), and black-tailed jackrabbits (*Lepus californicus*) because these species are the primary prey of Ferruginous Hawks in the Uintah Basin (Stalmaster 1988, H. Keough unpubl. data).

We also conducted nocturnal road surveys as an additional measure of lagomorph abundance around each nest. Using ArcView, we randomly selected two points that were >3 km apart from each other and <4 km from the nest. We then located the nearest good road (e.g., graded, paved, or two-track roads) to each point. Each nocturnal road survey was 2 km in length and began where the road was closest to the randomly selected point. The direction of road-transects was selected systematically to ensure all transects occurred within 4 km of each nest and that any overlap among transects was minimized. From 2100 to 2300 H, we drove along the road transect at 8 km/hr. Using the illumination provided by the vehicle’s headlights, we recorded the number of jackrabbits and cottontails observed during each transect.

All line-transects and road-transects were sampled twice for all nests; once between late May and late June and once between early July and early August.

We determined the total number of prairie dogs and lagomorphs seen during line-transects and road-transects for each nest and used these as indices of prey abundance (Table 1).

We determined raptor nesting activity during June and July, 2002–2004 by visiting all known nests for raptors larger than an American Kestrel (*Falco sparverius*) that occurred within 4 km of each nest to evaluate nesting activity. Using ArcView, we measured the distance from each nest site to the nearest occupied raptor nest occupied by Ferruginous Hawks, Red-tailed Hawks, Golden Eagles, Prairie Falcons, or Great Horned Owls (Table 1). Because competitive interactions may vary among raptors due to differences in resource availabilities, we measured the number of other occupied raptor nests that occurred within 1-, 1.5-, 2-, 2.5-, 3-, 3.5-, and 4-km radii of each nest. We also recorded the number of raptors, larger than an American Kestrel, observed during each line-transect prey survey, as a measure of raptor activity. We calculated the total number of raptors seen during all line-transects for each nest. We ignored any Ferruginous Hawks that we saw at the nest site but counted any seen soaring or hunting elsewhere.

The BLM supplied an ArcView database that included well type and status listings for all oil and gas well developments in the study area (Bureau of Land Management 2005). In collaboration with

the BLM Vernal Field Office, these data were categorized into active and inactive wells based on associated human activity levels. The active categories included: active drilling, producing gas well, producing oil well, water disposal well, water disposal well shut-in, water injection well, water injection well shut-in, water source well, and water source well shut-in. Using ArcView, we measured the distance from each nest site to the nearest active well. Because sensitivity to disturbance may vary among individuals, we measured the number of active wells that occurred within 1-, 1.5-, 2-, 2.5-, 3-, 3.5-, and 4-km radii of each nest (Table 1).

Data Analysis. Ferruginous Hawks show fidelity to nest sites, so nest attempts at the same nest site over multiple years do not represent independent samples. In our study, seven nest sites were occupied for multiple years. To avoid pseudo-replication, we used only data on reproduction and dependent variables that were collected during a single year for these seven nests in the classification and discriminant analysis. Data collected from these nests in other years were ignored.

We calculated four measures of reproductive success using all nests found over three breeding seasons to enable comparisons with previous and future studies: (1) the proportion of occupied nests that produced at least one nestling, one fledgling, or one dispersed young; (2) the mean number of nestlings, fledglings, and dispersed young per occupied nest; (3) the proportion of nestlings that successfully fledged; and (4) the proportion of fledglings that successfully dispersed. We determined the proportion of juvenile mortalities caused by depredation by birds, mammals, or unknown predator; natural causes; and unknown causes. We also described adult mortalities.

Classification and discriminant analyses were used to determine which of the nine variables measured best differentiate: (1) occupied nests that produced zero, one, two, three, or four nestlings; (2) occupied nests that produced zero, one, two, three, or four fledglings; and (3) occupied nests that produced zero, one, two, or three, dispersed young (Table 1). Because we had a numeric response variable, a mixture of continuous and categorical explanatory variables, missing data values (e.g., road surveys were not conducted in 2002), and relationships between variables that were likely to be nonlinear or involve high-order interactions, we chose to analyze the data using regression trees because they are ideally suited for analyzing such data (Clark and Pregibon

1992, De'ath and Fabricius 2000) and have been used previously with data from Ferruginous Hawks (Keough 2006, Keough and Conover 2012), Bald Eagles (*Haliaeetus leucocephalus*; Grubb and King 1991), and other avian species (Kavanagh and Bamkin 1995). This statistical method uses a computer-intensive algorithm that examines all variables to produce a sequence of binary splits (called a tree) that have the most predictive power and the lowest predictive error. Variables not selected in the tree may have had some effect, but they did not decrease the predictive error as much as those variables employed to construct the tree.

To select a single "best" model for each tree, we followed the methodology suggested by De'ath and Fabricius (2000). For each tree, we ran a series of 50 10-fold cross-validations and selected the most frequently occurring tree size using the minimum cross-validated-error rule. The models selected by cross-validation can be interpreted as the trees which had the smallest estimated true (prediction) error and were the "best" estimated predictive trees (De'ath and Fabricius 2000). All analyses were run using the Mypart Package Version 1.0-1 (De'ath 2004) in R Version 2.1.0 using the cross-validation method, with $xv = \text{"pick"}$, complexity parameter $cp = 0.001$, and the remaining default settings (R Development Core Team 2005). Once the three "best" trees were selected, we determined the proportion of the total sum of squares explained by each tree.

RESULTS

We located 31 occupied Ferruginous Hawk nests during the three breeding seasons (10 in 2002; 10 in 2003; 11 in 2004). Occupied nests were located on juniper trees (16), pinnacles (6), cliffs (5), human-made structures (3), and on the ground (1). Concomitantly, we found 71 other occupied raptor nests that were of species larger than an American Kestrel: 40 Red-tailed Hawk nests (12 in 2002, 11 in 2003, and 17 in 2004); 22 Golden Eagle nests (three in 2002, seven in 2003, and 12 in 2004); eight Prairie Falcon nests (one in 2002, two in 2003, and five in 2004); and one Great Horned Owl nest in 2004.

Reproductive Success. During the three breeding seasons, we monitored 31 occupied Ferruginous Hawk nests through dispersal. Twenty-two of the 31 occupied nests produced at least one nestling, 17 produced at least one fledgling, and 15 produced at least one dispersed young. An average of 1.87 nestlings ($SE = 0.26$), 1.32 fledglings ($SE = 0.26$), and

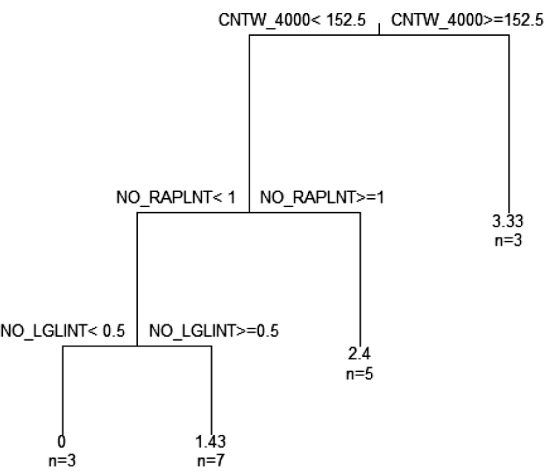


Figure 2. “Best” regression tree differentiating occupied Ferruginous Hawk nests that produced zero, one, two, three, or four nestlings. Occupied nests were located within the Uintah Basin, eastern Utah, during three breeding seasons (2002–2004). The explanatory variables were count of active wells within 4 km (CNTW_4000), number of raptors observed on line-transects (NO_RAPLNT), and the number of lagomorphs observed on line-transects (NO_LGLINT). The three splits (nonterminal nodes) are labeled with the explanatory variable and its values that determine the split, and the four leaves (terminal nodes) are labeled with the mean number of nestlings and the number of occupied nests in the group. The tree explained 59% of the total sum of squares ($R^2 = 1 - \text{Error}$), and the vertical depth of each split is proportional to the variation explained (CV Error = 2.02, SE = 0.51).

0.87 dispersed young (SE = 0.18) were produced per occupied nest. Of the 58 nestlings produced during the three breeding seasons, all of which were fitted with tarsal-mounted transmitters, 41 successfully fledged. Twenty-seven of the 41 fledglings successfully dispersed.

We recorded 31 juvenile mortalities (17 nestlings; 14 fledglings); 55% (10 nestlings; seven fledglings) were due to avian depredation, 16% (five fledglings) to mammalian depredation, 10% (three nestlings) due to depredation by an unknown predator, 16% (four nestlings; one fledgling) due to other natural causes (i.e., injury, exposure, disease, starvation), and 3% (one fledgling) due to unknown causes. Forty-one percent of juveniles depredated by avian predators were not eaten. We also located three adult carcasses. One adult was killed by an avian predator, based on wounds caused by talons, and the other two died of unknown causes. Field observations and wounds caused by large talons

indicated that most avian depredation events were carried out by large *Buteo* species, Great Horned Owls, or Golden Eagles. In 2004, we tracked a mortality signal from a transmitter to an occupied Golden Eagle nest, providing additional evidence that this species was one of the avian predators. The dimensions of talon markings on several depredated nestlings indicated that some predation events may have been carried out by adult Ferruginous Hawks or Red-tailed Hawks. In one of these instances, the depredated nest was located approximately 1.9 km from another occupied Ferruginous Hawk nest and none of the juveniles killed were eaten, suggesting that intraspecific competition for space was a possible explanation for the predation event. Mammalian predation events were most likely carried out by coyotes because they were the only mammalian predator that was regularly seen during our surveys.

Factors Associated with Reproductive Success.

During our line-transects, we observed a mean of 4.7 (11.3 = SD) prairie dogs and 4.3 (4.3) lagomorphs along the 2-km by 2-km squares (8 km total transect length) centered around each site. During our road-transects, we observed a mean of 4.7 (5.5) lagomorphs along the 2-km transect established for each nest.

The “best” regression tree differentiating nests that produced zero, one, two, three, or four nestlings included four leaves (three splits; Fig. 2). The explanatory variables that determined the three splits in the tree were the number of active wells within 4 km of the nest site (CNTW_4000), the number of raptors seen on line-transects (NO_RAPLNT), and the number of lagomorphs seen on line-transects (NO_LGLINT). Occupied nests with more than 152 active well sites within 4 km of them produced more nestlings ($\bar{x} = 3.3$ nestlings per occupied nest; $n = 3$ occupied nests) than nests with fewer active well sites ($\bar{x} = 1.5$ nestlings; $n = 15$). Occupied nests also produced more nestlings when we saw more than one raptor during each line-transect ($\bar{x} = 2.4$ nestlings; $n = 5$) vs. when no raptors were observed ($\bar{x} = 1.0$ nestlings; $n = 10$) and at least one lagomorph or prairie dog per line-transect ($\bar{x} = 1.4$ nestlings; $n = 10$) vs. ($\bar{x} = 1.0$ nestlings; $n = 3$) when no prey were seen.

The “best” tree differentiating nests that produced zero, one, two, three, or four fledglings included three leaves (Fig. 3). The explanatory variables that determined the two splits were the count of active wells within 1.5 km (CNTW_1500) and

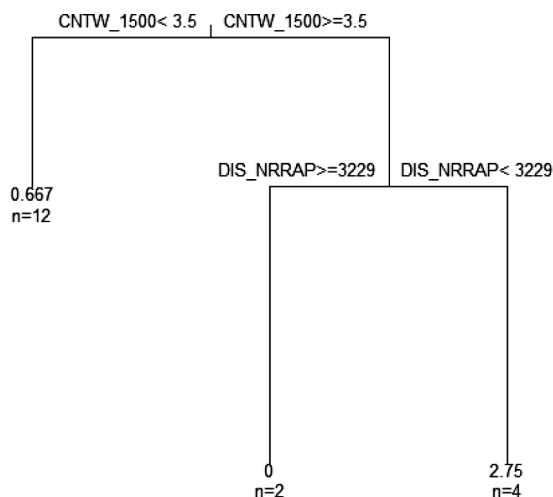


Figure 3. “Best” regression tree differentiating occupied Ferruginous Hawk nests that produced zero, one, two, three, or four fledglings. Occupied nests were located within the Uintah Basin, eastern Utah, during three breeding seasons (2002–2004). The explanatory variables were count of active wells within 1.5 km (CNTW_1500) and the distance to the nearest other occupied raptor nest (DIS_NRRAP). The two splits are labeled with the explanatory variable and its values that determine the split, and the three leaves are labeled with the mean number of fledglings and the number of occupied nests in the group. The tree explained 58% of the total sum of squares ($R^2 = 1 - \text{Error}$), and the vertical depth of each split is proportional to the variation explained (CV Error = 2.15, SE = 0.43).

distance to the nearest occupied raptor nest (DIS_NRRAP). Occupied nests with four or more active wells within 1.5 km of them produced more fledglings ($\bar{x} = 1.8$ fledgling per occupied nest; $n = 6$ occupied nests) than nests with fewer wells ($\bar{x} = 0.7$ fledglings; $n = 12$). Occupied nests that had another raptor nest within 3.2 km of them fledged more young ($\bar{x} = 2.8$ fledglings; $n = 4$) than nests which did not have a raptor nest so close ($\bar{x} = 0.0$ fledglings; $n = 2$).

Three leaves were included in the “best” tree differentiating nests that produced zero, one, two, or three dispersed young (Fig. 4). The two splits were determined by the count of active wells within 1.5 km (CNTW_1500) and distance to the nearest occupied raptor nest (DIS_NRRAP). Occupied nests with four or more active wells within 1.5 km of them produced more dispersed young ($\bar{x} = 1.5$ young per occupied nest; $n = 6$ occupied nests) than nests with fewer wells near them ($\bar{x} = 0.3$ young; $n = 12$). Occupied nests which had another

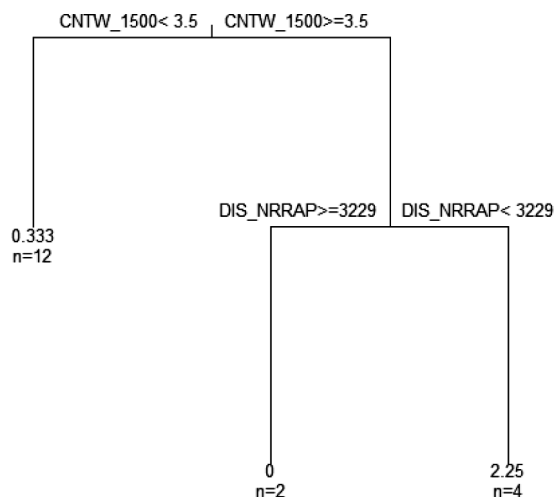


Figure 4. “Best” regression tree differentiating occupied Ferruginous Hawk nests that produced zero, one, two, or three dispersed young. Occupied nests were located within the Uintah Basin, eastern Utah, during three breeding seasons (2002–2004). The explanatory variables were count of active wells within 1.5 km (CNTW_1500) and the distance to the nearest other occupied raptor nest (DIS_NRRAP). The two splits are labeled with the explanatory variable and its values that determine the split, and the three leaves are labeled with the mean number of dispersed young and the number of occupied nests in the group. The tree explained 69% of the total sum of squares ($R^2 = 1 - \text{Error}$), and the vertical depth of each split is proportional to the variation explained (CV Error = 2.21, SE = 0.57).

raptor nest within 3.2 km of them had more dispersed young ($\bar{x} = 2.3$ young; $n = 4$) than nests which did not have a raptor nest so close ($\bar{x} = 0.0$ young; $n = 2$).

The “best” trees differentiating levels of reproductive success in terms of the number of nestlings, fledglings, and dispersed young produced had R^2 values of 0.59, 0.69, and 0.58, respectively. The models suggest that greater reproductive success is associated with: (1) nest attempts located in areas with higher counts of active well sites, and (2) nesting attempts in areas with relatively higher levels of raptor activity, such as higher numbers of raptors seen during line-transects and closer proximity to an occupied raptor nest.

DISCUSSION

Reproductive Success. The reproductive success of Ferruginous Hawks that we recorded during the three breeding seasons was similar to estimates re-

ported by other studies in the Intermountain West. The percentage of nesting attempts that produced at least one nestling (71%) was within the range (26–89%) reported by Stalmaster (1988) in Utah and Colorado, and within the range (58–71%) reported by Zelenak and Rotella (1997) in Montana. In addition, the percentage of nesting attempts in our study that produced at least one fledgling (55%) was within the range (34–67%) reported by Ward (2001) in Utah's West Desert, and within the range (26–85%) produced in Montana (Ensign 1983, Restani 1989, Van Horn 1993, Zelenak and Rotella 1997). The average number of nestlings (1.9) produced per occupied nest that we observed was within the 0.4–3.1 range of yearly means observed by Stalmaster (1988), the yearly means of 1.7–2.3 observed by Ward (2001), and close to the average of 1.7 reported by Zelenak and Rotella (1997). Also, the average number of fledglings (1.3) produced per occupied nest that we observed was within the yearly range (\bar{x} = 0.6–1.9) noted by Ward (2001). Lastly, the average number of dispersed young (0.87) produced per occupied nest that we observed was similar to the average (0.82) reported in Montana (Zelenak et al. 1997).

The similarities between the reproductive success reported by this study and previous studies in the Intermountain West are surprising given that the Uintah Basin experienced a drought during our entire study period. We expected the drought to reduce prey availability and increase competition for resources, subsequently resulting in lower reproductive success. We observed no lagomorphs during 35% of line-transect surveys and 43% of road-transect surveys; we also did not see any prairie dogs during 61% of line-transect surveys. These results suggest overall low prey abundance. In addition, depredation by avian predators was the primary cause of juvenile mortalities, suggesting a highly competitive environment.

The prevalence of avian predation during the three breeding seasons may have resulted from competition for space. The fact that 41% of juveniles depredated by avian predators were not eaten suggests that many attacks were probably not motivated by hunger. Depredation was also the primary cause of juvenile mortality for Ferruginous Hawks in western Utah during 1997–1999 (Ward and Conover 2013). Approximately 60% of all predation events they documented were attributed to avian predators, with the majority of predation events attributed to Golden Eagles. As the abundance of

lagomorphs decreased over the 3-yr study period, avian predation on juvenile Ferruginous Hawks increased, possibly a result of Golden Eagles utilizing juvenile Ferruginous Hawks as an alternative prey source when lagomorph abundance is low (Ward and Conover 2013). Golden Eagles are known to eat Ferruginous Hawks, as well as many other raptor species (Ellis et al. 1999, Kellert 2000). Although juvenile Ferruginous Hawks may provide an alternative prey source, Golden Eagles risk injury from adult Ferruginous Hawks when attempting to capture nestlings and fledglings (Ward 2001). As such, Golden Eagles likely risk preying upon juvenile Ferruginous Hawks only when lagomorph abundance is low (Ward 2001).

Mammalian predators only killed fledglings during our study. Bechard and Schmutz (1995) reported that coyotes, badgers, and foxes might represent a serious threat to ground nests and fledglings. Because 25 of the 31 occupied nests (81%) in our study were elevated, they were less accessible or inaccessible to mammalian predators, so it is not surprising that we found no nestlings depredated by coyotes. However, fledglings may also be more susceptible to mammalian predation because nestlings often leave the nest before they can fly, which might make newly fledged young relatively easy to capture.

Data on juvenile Ferruginous Hawk survival after fledging are relatively rare. When reported, post-fledgling survival rate is high (72–92%; Konrad and Gilmer 1986, Restani 1989, Zelenak et al. 1997, Ward and Conover 2013). However, in our study, only 66% of fledglings successfully dispersed. Had we assumed all fledglings successfully dispersed, we would have overestimated reproductive success and underestimated the effect of predation.

Factors Associated with Reproductive Success.

We predicted *a priori* that Ferruginous Hawk nests would be more successful if located on elevated substrates (e.g., juniper tree, rock pinnacle, human-made structure), but we found that elevated nests were no more successful than ground nests. We also predicted that reproductive success would be higher in areas with abundant prey. Interestingly, we found a positive association between the production of nestlings and the abundance of lagomorphs, but not of prairie dogs. Previous researchers found positive relationships between Ferruginous Hawk nest success and prey abundance (Smith et al. 1981, White and Thurow 1985, Stalmaster 1988, Woffinden and Murphy 1989, Zelenak and Rotella 1997,

Ward 2001, Dechant et al. 2003). Greater abundance of lagomorphs near the nest may be more important at the nestling stage than at later stages, as the young are growing fast and require large amounts of food (Keeley 2009).

We expected the threat of avian predation would be reduced, and thus reproductive success would be higher, in areas with lower levels of raptor activity. Instead, we found the opposite: greater reproductive success was associated with higher levels of raptor activity (e.g., more raptors observed during line-transects and more raptor nests nearby). Perhaps this relationship is simply a spurious correlation, resulting because both raptor activity and Ferruginous Hawk reproductive rate were positively associated with lagomorph abundance. Hence, nests with more raptor activity near them may simply be nests located in habitat with more abundant prey, and this may explain why such nests produce more nestlings.

The positive association between reproductive success and the distance to another occupied raptor nest may be explained by the same correlation of both with lagomorph abundance. Raptors often nest in higher densities in areas with higher prey densities. In Alberta, Canada, Ferruginous Hawks and Swainson's Hawks (*Buteo swainsoni*) chose to settle in optimal habitat rather than suboptimal habitat, and additions of new settlers resulted in smaller average territory sizes in optimal habitat (Schmutz 1989). Individuals defending small territories in optimal habitat might have access to more resources and have greater nest success than individuals defending large territories in suboptimal habitat (Schmutz 1989). Other studies found Ferruginous Hawks nesting <3.4 km of the nearest other raptor nest (Lokemoen and Duebbert 1976, Smith and Murphy 1978, Olendorff 1993).

We predicted that oil well development would have an adverse effect on the reproductive success of Ferruginous Hawks. Instead, reproductive success was higher in areas with higher densities of active wells than in areas with fewer wells. This correlation may reflect the quality of the habitat surrounding wells, or the ease of foraging in a landscape with more perch sites. Presence and higher abundance of raptors have been associated with increased number of perch sites (Behney et al. 2012). Our results were similar to those of Zelenak and Rotella (1997), who found Ferruginous Hawks nesting in habitats altered by humans produced more young, potentially as a result of increased prey of Richardson's ground squirrels (*Urocitellus richardsonii*). In studies

at energy development sites in Montana and Wyoming, Ferruginous Hawk productivity was not influenced by the distance of active wells to the nest or the density of active wells, but rather by the density of ground squirrels (Van Horn 1993, Wallace 2014).

Our results indicate that the level of oil well development that occurred at the time of our study did not have an adverse effect on the reproductive success of Ferruginous Hawks. The effect of a higher level of oil development was beyond the scope of this study. Other researchers have suggested creating buffer zones ranging from 0.25–1 km from occupied nest sites during human activities to minimize disturbance to breeding Ferruginous Hawk pairs (Suter and Jones 1980, White and Thurow 1985, Atkinson 1992, Olendorff 1993, Keeley and Bechard 2011).

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