NESTING ECOLOGY OF RAPTORS IN NORTHWEST UTAH: 1998–2007

HawkWatch International
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INTRODUCTION

HawkWatch International (HWI) conducted annual raptor nest surveys in northwestern Utah from 1998–2007 under primary sponsorship of the Utah Division of Wildlife Resources (UDWR) and Bureau of Land Management–Salt Lake Field Office (BLM-SLFO). Our primary objective was to provide land managers with baseline raptor inventory and nest-monitoring data from the region and establish a scientifically defensible basis for making management decisions that help maintain ecosystem integrity and the area's nesting raptors. HWI previously prepared annual reports summarizing each year's survey results; this report represents the first comprehensive, GIS-based assessment of the data collected. The specific objectives of this report are:

1) Describe the general vegetation, fire, and climatic conditions within the study area during the survey years.
2) Describe the basic characteristics of raptor nesting territories and associated nests within the study area, emphasizing seven focal species.
3) Assess regional densities of raptor territories and territory activity, as well as annual patterns in focal species territory occupancy and activity, laying dates, nest success, and productivity.
4) Assess the influence of landscape, climate, and nest-site variables on territory activity, nest success, and productivity for all focal species, where applicable.
5) Discuss implications relative to management and conservation of diurnal raptors and Burrowing Owls ((*Athene cunicularia*) in this region of the northern Great Basin.

METHODS

Our study area in northwestern Utah was roughly bounded to the south by I-80, to the north by the Idaho border, to the west by the Nevada border, and to the east by the western margins of the Great Salt Lake (Figure 1). The study area is part of the Great Basin physiographic region and the Central Basin and Range ecoregion. Within this area, our work emphasized seven focal raptor species that are characteristic of the cliff, open woodland, and shrubsteppe habitats common to this area of the northern Great Basin: Golden Eagle (*Aquila chrysaetos*), Ferruginous Hawk (*Buteo regalis*), Swainson's Hawk (*B. swainsoni*), Red-tailed Hawk (*B. jamaicensis*), Peregrine Falcon (*Falco peregrinus*), Prairie Falcon (*F. mexicanus*) and Burrowing Owl. Monitoring the Ferruginous Hawk and Burrowing Owl is of particular importance because these species are listed as a Wildlife Species of Concern in Utah. When we began this survey in the late 1990s, the Swainson's Hawk also was listed as a species of concern in Utah and it is still recognized as a Partners in Flight (PIF) Continental Watch List species. Although Golden Eagles are not yet afforded any special status, long-term nesting studies in the Snake River region of Idaho and in north-central Utah, as well as regional migration-count indices, confirm significant declines in nesting activity and overall populations, with large-scale loss and degradation of native shrubsteppe habitat believed to be the principal cause of declines in the Intermountain region. The project also addresses monitoring and research needs highlighted in the PIF North American Landbird Conservation Plan for the Basin & Range Physiographic Area wherein Ferruginous Hawks, Swainson's Hawks, and Prairie Falcons are recognized as priority species in relation to conservation of shrubsteppe, sagebrush grassland, and pinyon-juniper habitats.

Annual survey work typically occurred from 15 March through early August to encompass the majority of the nesting cycles of all focal species. Our objective was to visit each active nest at least three times during the season to document occupancy or "activity" (i.e., a nest start), hatching and initial brood size, and nesting success and fledgling production. Crews located active nests based on known nest records and by scanning suitable habitat for signs of nesting or adult activity. They recorded numerous nest and nest-site characteristics for each documented nest.

We grouped all raptor nests into territories based on their history of use, field knowledge, and inspection of nest spacing and configuration. We gathered and refined elevation, vegetation (based on Southwest ReGAP datasets), fire, and climate map layers, and annual climate data available for the study area. We used basic statistics and graphs to describe the general study area characteristics, territory and nest characteristics, nest fidelity, annual egg laying dates, and regional and annual demographic trends. We used ArcMap to quantify local (within a 2-km radius) vegetation and landscape characteristics, compare all raptor territories to the random study area, and compare territory characteristics of the focal species.

We defined three spatial scales of research interest for each focal species (excluding the Peregrine Falcon, due to small sample size), based on apparent selection scales within the study area (examined across 10 spatial scales [0.5-5.0-km radius, 0.5-m increments], and average and upper home-range sizes as suggested by literature review. We used model-selection techniques to identify landscape (i.e., vegetation and elevation) variables measured at the study area, average home range, and/or upper home range scales, as well as climate (annual and seasonal drought-severity and temperature indices) and/or nest-site (elevation, average site precipitation, numbers of alternate nests, and/or site aspect, nest height, or nest substrate) variables influential to annual territory activity (nest starts), proportional territory activity (i.e., the proportion of survey years a nest/territory supported a nest start), nest survival, and nest productivity. [Note: adequate treatment of the definitions and calculations of the explanatory variables and response metrics is beyond the scope of this summary, but is provided in the actual report]. For each response metric, we used stepwise procedures to identify potential informative logistic-regression, multiple-regression, or logistic-exposure (*sensu* Shaffer 2004) models, and Akaike's information criterion (AICc) to identify the "top" predictive models (Burnham and Anderson 2002).

RESULTS AND DISCUSSION

The study area is dominated by desert shrub, sagebrush, and grass/forb vegetation, with pinyon-juniper (*Pinus edulis* or *monophylla – Juniperus* spp.) the most common woodland vegetation type. Human development and dryland and irrigated hayfield and improved pasture habitats comprise a relatively small but influential portion of the landscape. Drought conditions dominated the 1998–2007 study period and peaked in 2003. Fires were most common in the early and late study years following wet periods. Although at least 92 known raptor nests were located within fire boundaries, only about 10% of these nests were destroyed due to the location of most on low-fire-risk substrates. The static nature of the vegetation datasets available for incorporation in our analyses precluded more effective investigations of relationships between fire history, habitat change, and raptor nesting ecology.

Golden Eagles, Prairie Falcons, and Peregrine Falcons nested predominantly on cliff and other rocky substrates. Ferruginous and Swainson's Hawks nested mostly in junipers. Red-tailed Hawks used a broad array of cliff/outcrop, tree, and manmade substrates. Red-tailed and Swainson's Hawk nests were found disproportionately on private land, likely related to the presence of planted nest trees and agricultural lands. Red-tailed Hawks averaged significantly higher nest-site elevations than all other species, while Burrowing Owl nest-sites averaged significantly lower. Ferruginous Hawk nests were higher than Burrowing Owls, but lower than all other species. Golden Eagle, Swainson's Hawk, and Prairie Falcon nest-site elevations were similar. Red-tailed Hawk and Golden Eagle nests were spread across the broadest range of elevations and were found at the highest elevations, Burrowing Owl nests spanned the narrowest range, and Prairie Falcons spanned a moderate range of elevations.

Excluding Peregrine Falcons (only 2 nests known) and Burrowing Owls (all burrows considered independent entities for practical simplicity), all focal species used both single and multiple-nest territories. Alternate nests within individual territories average 300–600 m apart across all species, but were often as little as meters apart. Focal species often (>35% of the time) used the same nest or borrow in consecutive years, but it also was common (i.e., >10–30% of the time) for three or more years to pass between nest starts at an individual nest. These results reinforce the need for adequate temporal protection of inactive nests.

The density of all known raptor territories in the study area was roughly 4.1 territories per 50 km^2. Estimated species-specific densities tended to suggest relatively low to at best moderate densities compared to most previous studies in Utah and surrounding states. Overall densities were particularly high in the Grassy/Lakeside Mountains, Raft River Mountains, and Grouse Creek Valley and Mountains regions. Proportional activity was also relatively high in the latter two regions and decreased from north-to-south across the study area, likely related to a general decrease in elevation and moisture in this direction. The Grouse Creek Valley and Prohibition Springs areas were hot spots of raptor territory activity, likely due to the combinations of habitat and especially prevalence of irrigated agriculture and improved pasture habitats in these areas.

Territory occupancy and activity were relatively high between 2001–2007 (sample sizes were limited in the first three years) for the Golden Eagle, Red-tailed Hawk, Swainson's Hawk, and Prairie Falcon, relative to the Ferruginous Hawk and Burrowing Owl (occupancy only). We speculate that an apparent decline in Burrowing Owl proportional occupancy (% of checked burrows occupied) through the survey period likely was an artifact of survey design and treatment (i.e., a burrow-centric rather than territory focus), with the actual numbers of occupied burrows remaining comparatively stable from 2001–2007. Nest success peaked in 2006 for the Golden Eagle, Ferruginous Hawk, and Prairie Falcon. Fledgling production (per nest start) was highest in 2005, the wettest year of the 2001–2007 analyzed period, with only a slight decline in 2006 for these species, as well the Swainson's Hawk. It appeared that all species showed a positive and sometimes lagged (by one year) response to the wettest survey year (2005), which followed several years of severe drought.

We report annual and average egg-laying dates for all relevant focal species for the period 2001–2007. Laying generally occurred progressively earlier from 2001–2005, then began to retreat again slightly between 2006 and 2007. The general pattern suggested earlier nesting in both the driest (2003) and wettest (2005) years of the study, and species-specific analyses of nest-site and climatic correlates suggested a complex picture. Neither simple, univariate linear regressions nor integrated multiple regression models suggested that year, nest-elevation, or climate variables explained statistically significant ($P > 0.05$) components of variation in laying dates for Ferruginous and Swainson's Hawks. In contrast, Golden Eagle laying dates averaged significantly later at overall wetter (long-term average site precipitation) nest sites and following colder winters (i.e., higher winter snowpack delays nesting), but earlier in later years. Red-tailed Hawks nested later at higher elevations and following wetter winters, but earlier during less drought-stricken nesting seasons and in later years. Similar to Golden Eagles, Prairie Falcons also tended to nest later in wetter areas.

At the combined-species level, raptors territories averaged more big sagebrush (*A. tridentata*), semi-desert shrub/grass, and agriculture within a 2 km radius than the landscape as a whole. Golden Eagle and Prairie Falcon territories were similar and contained more cliff and canyon, barren, playa/wash, and semi-desert vegetation than the landscape as a whole and compared to other species. Ferruginous and Swainson's Hawk territories both contained more agriculture and big sagebrush, and Ferruginous Hawk territories contained more invasive vegetation (primarily cheatgrass [*Bromus tectorum*]). Red-tailed Hawk territories were characterized by more pinyon-juniper, montane sagebrush shrub, riparian vegetation, and human development. Burrowing Owl burrows were associated with more invasive vegetation and mixed salt desert scrub.

Overall for the focal species, landscape variables (measured at multiple scales), climate, and nest-site variables performed poorly as predictors of annual territory activity (occupancy for Burrowing Owls) and nest productivity (McFadden's ρ^2 or adjusted r^2 <10%), whereas proportional activity models (occupancy for Burrowing Owls) consistently performed the best of the analyzed model types (adjusted r^2 >10%) and performed particularly well for the Red-tailed Hawk and Prairie Falcon (adjusted r^2 >30%). The difference likely reflects the fact that interannual variability in nesting activity and/or success/productivity among individual breeding pairs is relatively high and influenced by a broad array of individual-behavior as well as landscape variables. As a result, average tendencies assessed over extended periods may better capture influential relationships with landscape-level variables such as overall climatic regimes and static habitat coverage maps. Various nest-site variables were most influential to proportional activity for the Golden Eagle (positive correlation with number of nests), Swainson's Hawk (positive correlations with number of nests, nest-site elevation, and average site precipitation), Prairie Falcon (positive correlation with number of nests and negative correlation with site "ruggedness"), and Burrowing Owl (positive correlation with nest-site elevation and negative correlation with site ruggedness). Various landscape variables were most influential to proportional activity for the remaining focal species. Although not as good as the performance of proportional activity models, nest survival models also performed fairly well (McFadden's ρ^2 >10%) for all but the Golden Eagle and Red-tailed Hawk.

We found that landscape, climate, and nest-site variable groups all were important at some level for particular species and/or model types. Relationships with landscape variables were not consistently best described at one particular scale for the various metrics or species, and relationships detected at more than one scale for a particular metric (e.g., proportional activity) were not necessarily consistent across scales. We found that human-influenced landscapes, including invasive vegetation, significantly influenced all focal species in some way, but with the documented relationships typically mixed and complex. For example, our results suggested that both Ferruginous Hawks and Burrowing Owls occupied habitats that featured proportionately more invasive cheatgrass vegetation than the landscape as a whole and compared to other species, but their nesting activity and/or success/productivity levels in these habitats were below average. Similarly, the annual and proportional activity models for Red-tailed Hawks consistently indicated positive associations with human development and agriculture, but this positive association did not translate to similar indicators in the nest-survival and productivity models for the species.

CONCLUSIONS AND MANAGEMENT IMPLICATIONS

Our results stress the importance of a territory focus for the monitoring and/or protection of nesting raptors, as individual nests typically are not independent entities. Additionally, our documentation of both regular inter-annual nest fidelity and gaps in activity of three or more years has important implications for the management of individual nests. Our results suggest that extending 5-years of protection to inactive nests (from the last documented activity) may be a reasonable management prescription; however, longer between-use intervals are fairly common. *More importantly, we strongly encourage adoption of standards that stipulate equivalent protection for all known alternate nests within a territory regardless of which nest was used most recently.*

Our work in northwest Utah highlights the difficulties of adequately monitoring Burrowing Owls with typical, community-level raptor nest-monitoring protocols. Due to their colonial and subterranean habits, the territory dynamics of Burrowing Owls are difficult to establish without prolonged observations and marking individuals, and as a result we were forced to consider each burrow as an independent unit rather than being able to identify individual territories as containing a series of alternate nest sites. This undoubtedly was at least partially responsible for the declining occupancy trends we reported for this species across survey years, as individuals likely switched between burrows over time. We suggest that, in the absence of a more advanced understanding of individual territory dynamics, surveyors focus on the overall occupancy, activity, etc. of entire "burrow complexes" (i.e., spatially clumped burrows distinct from other burrow clumps).

We suggest that local land managers pay particular attention to the relatively high raptor nesting activity in the Grouse Creek Valley and Prohibition Springs area, and consider educating local private landowners about the importance of their lands for nesting raptors.

Our results suggest that the severe drought that plagued the study area and most of the Intermountain region during our study period did not greatly affect the overall nesting activity levels of Golden Eagles, Red-tailed Hawks, Swainson's Hawks, and Prairie Falcons, whereas the overall density of nesting Ferruginous Hawks in the area more than doubled when moisture conditions rebounded at least temporarily in 2005/2006. Moreover, for all relevant species, apparent effects of the drought cycle on nesting success and productivity often were much more apparent. In addition, although most of the focal species did show some level of immediate, positive response to the 2005 spike in precipitation levels, that positive influence often was more or equally noticeable the following year despite a return to lower moisture levels that year. This suggests a delayed impact on prey abundance and availability. In similar fashion, it was noteworthy that fire was not most prevalent during the driest, peak drought years, but rather at the beginning of a dry cycle during the year or two immediately following a wet period when vegetation fuel loads were high.

Egg laying dates reported for the focal species did not differ consistently from values reported in previous studies conducted nearby 15–30 years earlier. Changes in our laying dates did correlate with survey-year, suggesting progressively earlier egg laying over time for Golden Eagles and Red-tailed Hawks, but the short duration of the analysis window (i.e., 7 years) and potential confounded relationship between year and moisture conditions preclude drawing strong conclusions from these results.

Our results suggested that, although relatively uncommon in our study area, human-influenced landscapes appeared to affect each focal species in some way, and we advocate, in particular, that additional research into the complicated relationships between invasive vegetation and Ferruginous Hawk and Burrowing Owl nesting ecology warrant further investigation. Our research also suggests that individual raptor species may respond to landscape characteristics at multiple and various scales, and we therefore discourage researchers from adopting a one-size-fits-all approach to scale-related investigations. Lastly, even the best of our models designed to describe the landscape correlates of raptor nesting activity in our study area explained substantially less than a majority of the variance in the datasets. Although not unexpected given the complexities of ecological systems, one major limitation of our work (a reflection of resource limitations) is the lack of information concerning prey abundance. Other similar long-term studies that have also been able to rigorously monitor patterns of prey abundance clearly emphasize the relevance of such data for understanding the primary drivers of raptor ecology in similar regions (e.g., Steenhof et al. 1997, 1999). Thus, our final management recommendation is that to further advance our collective, detailed understanding of the ecology of the northwest Utah raptor community will require the addition of an extensive and rigorous program to simultaneously monitor prey abundance in the region.

INTRODUCTION

HawkWatch International (HWI) conducted intensive annual raptor nest surveys in northwestern Utah from 1998 to 2007, with primary financial support for these efforts provided by the Utah Division of Wildlife Resources (UDWR) and Bureau of Land Management–Salt Lake Field Office (BLM–SFO). Each year, HWI prepared a report summarizing the results of these surveys and basic reproductive demographics for focal raptor species. The purpose of this document is to provide a more comprehensive assessment of the data collected during this 10-year period. More specifically, we sought to use Geographic Information System (GIS) layers, climate data, and statistical modeling to describe the general habitat and spatial characteristics of raptor territories and to investigate the potential influence of habitat and climate on reproductive demographic trends of focal raptor species.

SURVEY HISTORY AND GOALS

During spring 1998, HWI and selected members of the Utah falconry community conducted a pilot survey to begin documenting the distribution, density, and productivity of nesting Prairie Falcons (*Falco mexicanus*) in northwest Utah (Smith and Hoffman 1998). The following spring, HWI unilaterally expanded the geographic coverage and species diversity of the survey (Smith 2000a). The UDWR sponsored an initial planning meeting in 1998 and provided funding for the 1999 surveys. During spring 2000, acting under joint sponsorship of the UDWR and the BLM – SFO, HWI conducted a third and final year of pilot study (Smith 2000b) in anticipation of beginning a five-year standardized survey in 2001 (Smith 2001, 2002, 2003, 2005, Smith and Hutchins 2006a). Beginning in 2003 under new sponsorship of the Nevada BLM, HWI expanded the survey into northeastern Nevada, and completed the first two seasons of nest monitoring in this area in 2004 and 2005 (Smith and Hutchins 2005, 2006b). Funding limitations restricted the surveys to Utah in 2006 (Smith and Hutchins 2007), but both resumed in 2007 (Slater and Smith 2008, Smith and Slater 2008), providing the third annual survey of the larger Utah and Nevada study areas. In this report, however, we restrict our attention to the Utah survey effort for reasons of longer-term survey consistency.

We now refer to the larger, combined Utah–Nevada survey effort as our Great Basin Raptor Nest Survey (GBRNS). The primary goal of GBRNS has been to provide the UDWR, BLM, and other regional landowners and managers operating in the region with a comprehensive inventory of raptor nests and demographic data for focal raptor species in order to provide a scientifically defensible basis for making land-management decisions and developing land-management plans that maintain healthy populations of nesting raptors in the northern Great Basin. Such baseline information is essential for projecting the impacts of a variety of potential disturbances and changes to habitat and land use practices. Focusing on shrubsteppe and open woodland habitats meshes well with the UDWR's designation of rangeland as a focal habitat and expression of interest in improving management of Utah rangelands (UDWR 2000:21). More recently, the new Utah Comprehensive Wildlife Conservation Strategy (Sutter et al. 2005) further emphasizes priority concerns for improving management of shrubsteppe and grassland habitats. Having expanded into Nevada, the overall GBRNS effort similarly supports the Nevada Bird Conservation Plan strategy objectives for several identified raptor species that breed in cliff and talus, pinyon-juniper (*Pinus edulis* or *monophylla – Juniperus* spp.), and sagebrush (*Artemisia* spp.) habitats (Neel 1999).

OBJECTIVES

Herein, we present the first comprehensive, GIS-based analysis of the raptor nesting-ecology data collected in the study area between 1998 and 2007. The primary objectives of this report are as follows:

1) Describe the general vegetation, fire, and climatic conditions within the study area during the survey years.

2) Describe the basic characteristics of territories and associated nests of raptors within the study area, emphasizing seven focal species.
3) Assess regional densities of raptor nesting territories and territory activity, as well as annual patterns in focal species territory occupancy and activity, laying dates, nest success, and productivity.
4) Assess the influence of landscape, climate, and nest-site variables on territory activity, nest success, and productivity for all focal species, where applicable.
5) Discuss the implications of these analyses for the management and conservation of diurnal raptors and Burrowing Owls in this region of the northern Great Basin.

METHODS

FOCAL STUDY SPECIES

Our efforts focused on seven, primarily diurnal raptor species that nest on cliff or in open woodland and shrubsteppe habitats characteristics of the Great Basin: Ferruginous Hawk (*Buteo regalis*), Swainson's Hawk (*B. swainsoni*), Red-tailed Hawk (*B. jamaicensis*), Golden Eagle (*Aquila chrysaetos*), Prairie Falcon, Peregrine Falcon (*Falco peregrinus*), and Burrowing Owl (*Athene cunicularia*). Note, however, that during the study period the Peregrine Falcon was represented by only two nesting sites, only one of which was active more than once; hence, we devote little attention to this species in this report. Other generally less common nesting species that we encountered and monitored opportunistically included the Northern Harrier (*Circus cyaneus*), Cooper's Hawk (*Accipiter cooperii*), Northern Goshawk (*A. gentilis*), American Kestrel (*F. sparverius*), Long-eared Owl (*Asio otus*), Great Horned Owl (*Bubo virginianus*), Western Screech-owl (*Otus kennicottii*) , and Barn Owl (*Tyto alba*). We also monitored nesting Common Ravens (*Corvus corax*) because this species regularly uses the same nests as several raptor species.

Monitoring the Ferruginous Hawk is of particular importance because the species is listed as a Wildlife Species of Concern in Utah (UDWR 2004, also see Parrish et al. 2002). Moreover, prior to HWI's efforts, the UDWR and BLM, through a previously established cooperative agreement, had already invested considerable effort in documenting nesting by this species throughout the BLM – SFO (Doumitt et al. 2000). Our study provided a means of continuing this effort throughout roughly 25% of the SFO region. A similar level of importance can be attached to collection of data on the Burrowing Owl, which also is listed as a State Wildlife Species of Concern in Utah (UDWR 2004). When we began this survey in the late 1990s, the Swainson's Hawk also was listed as a species of concern in Utah, but was recently removed from the list in light of new data indicating that populations are at least stable if not increasing in the Intermountain region (England et al. 1997; and see Hoffman and Smith 2003, Smith et al. 2008). Nevertheless, the Swainson's Hawk still is recognized as a Partners in Flight (PIF) Continental Watch List species (Rich. et al. 2004). Although Golden Eagles are not yet afforded any special status, long-term nesting studies in the Snake River region of Idaho (United States Department of Interior 1996, Steenhof et al. 1997) and in north-central Utah (e.g., Keller 2006) confirm that nesting populations in these regions have shown significant declines in nesting activity and/or nest productivity (also see Hoffman and Smith 2003, Smith et al. 2008). Large-scale loss and degradation of native shrubsteppe habitat, which supports the eagles' primary prey species the black-tailed jackrabbit (*Lepus californicus*), is believed to be the principal cause of these declines (Knick and Dyer 1997). The project also addresses monitoring and research needs highlighted in the PIF North American Landbird Conservation Plan for the Basin & Range Physiographic Area wherein Ferruginous Hawks, Swainson's Hawks, and Prairie Falcons are recognized as priority species in relation to conservation of shrubsteppe, sagebrush grassland, and pinyon-juniper habitats (Rich. et al. 2004).

We began this project with knowledge of many historic nesting territories for the focal species derived from a database provided to us by the BLM – Salt Lake Field Office. This initial database contained records for 554 nest sites of the focal species in our survey area, with heavy emphasis on Ferruginous Hawks due to the prior efforts of Doumitt et al. (2000). Many of these nests no longer existed by the time we began our work, but by 2007 we had confidently located and updated the status records for the majority of these historic nests.

STUDY AREA

The northwestern Utah study area is roughly bounded to the south by I-80, to the north by the Idaho border, to the west by the Nevada border, and to the east by the western margins of the Great Salt Lake (Figure 1). The study area is part of the Great Basin physiographic region and the Central Basin and Range ecoregion. Salt desert shrubs and playa/wash dominant the low elevation areas, shrubsteppe and open pinyon-juniper woodlands dominant the foothills, and conifers and aspens (*Populus tremuloides*) are common at higher elevations. Cheatgrass (*Bromus tectorum*) has effectively replaced shrubs and native grasses at many low and mid-elevation sites, especially in areas following fire. We largely excluded from our surveys high-elevation, extensive conifer forests, which may harbor species such as the three North American members of the genus *Accipiter*, for practical reasons of logistical simplicity and resource limitation. Instead, we focused our surveys on the shrubsteppe, woodland, and cliff habitats that are particularly conspicuous elements of the Great Basin landscape and support most raptors that breed in the region.

The overall study-area landscape encompasses substantial areas of private land. Limited access to these private lands restricted our coverage of some important habitat areas. For example, private lands commonly contained dryland and irrigated hayfields, and improved pastures, and all of the focal buteo species, especially, are regularly drawn to such areas to forage and often nest nearby on private land. Although our survey crews generally did not attempt to gain access to private lands that were clearly posted, readily available landowner permission and public/private adjacencies afforded some monitoring of these areas. Livestock grazing (cattle and sheep) and various forms of recreational activity (primarily all-terrain vehicle touring and shooting) also routinely occur on both public and private lands across much of the study area.

For geographic summary purposes, we divided the study area into seven largely distinct survey regions based on the distribution of 7.5′ topographic quads: Silver Island Mountains (8 full quads and half of one UT/NV border quad), East and North Pilot Range and Adjacent Hills (8 full and half of 4 UT/NV border quads), Newfoundland Mountains (6 quads), Matlin/Hogup/Wildcat/Curlew Basin, (27 quads), Grouse Creek Valley and Mountains (15 full quads and half of 5 UT/NV border quads), Raft River Mountains (6 quads), and the Grassy and Lakeside Mountains (19 quads and small portions of 3 others located mostly south of I-80) (Figure 2).

To further define the boundaries of the actual survey area for analysis purposes, we first extended a 1-km buffer around all known nest sites, then eliminated from further consideration 1) all contiguous areas of non-potential-nesting habitat (i.e., playa/wash and water habitat types; classification scheme discussed below) that were not within the 1-km buffer areas around known nests, 2) large tracts (i.e., >1,000 ha) of potential vegetation that we were unable to survey due to private-property and military restrictions; and 3) areas of inaccessible (via established roads) habitat above 2,100 m elevation. This produced a 9,087-km² study area (Figure 1) encompassing 64% accessible public land, 35% private land, and 1% military land. The elevation in this study area ranged from 1,286–3,031 m (mean 1,532 m). Annual average precipitation in the area from 1998–2007 was 20.8 cm (NOAA 2008).

Our objective for the surveys from 2001–2005 was to accomplish a comprehensive census of focal-species nesting activity across all accessible areas of suitable habitat within the overall study area, subject to the caveat that our efforts were restricted to habitats accessible by established backcountry roads and

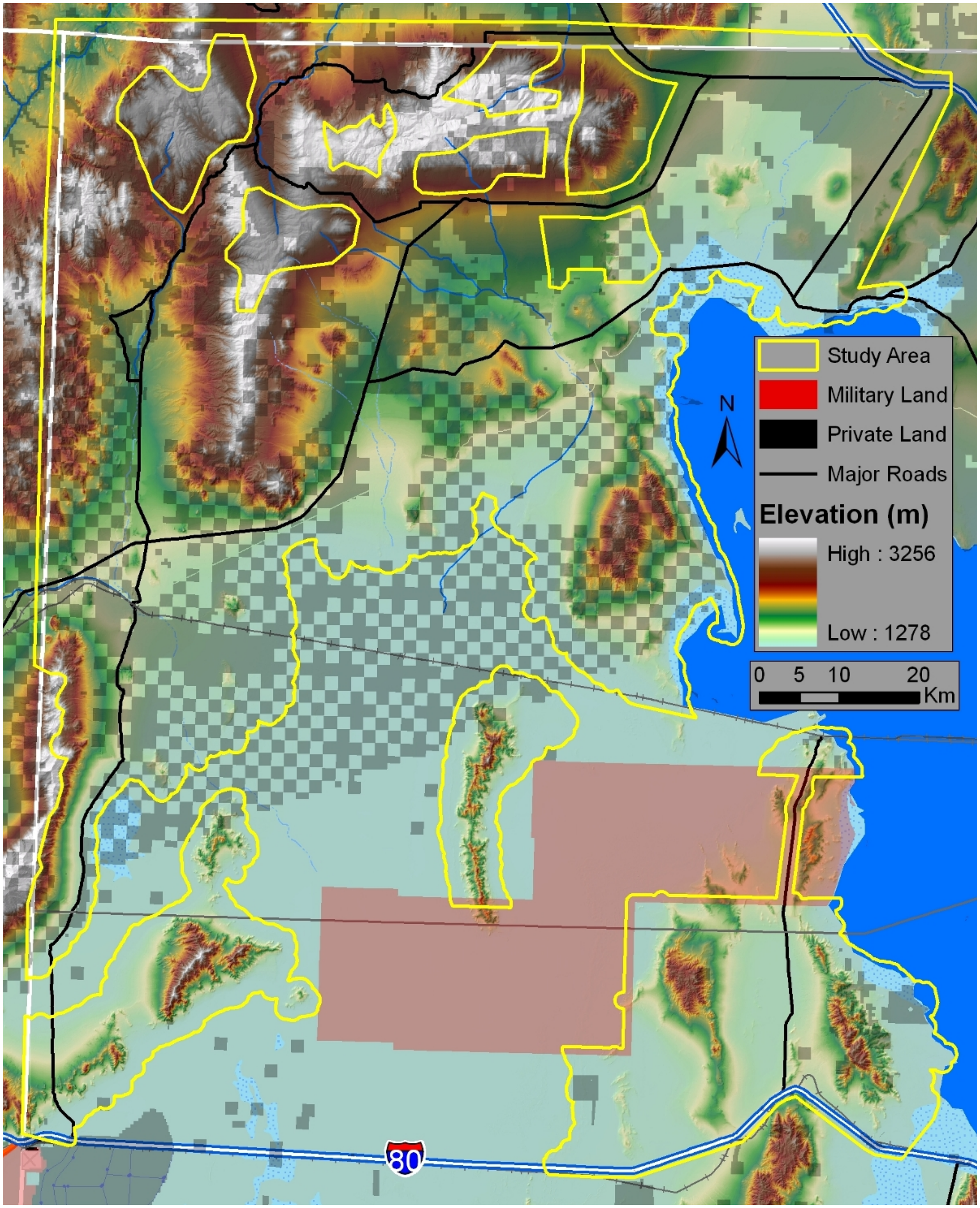

Figure 1. Northwestern Utah raptor nest survey study area boundaries refined by vegetation type, land ownership, elevation, and accessibility. The study area boundary generally represents the survey coverage for target habitats and focal species between 2001 and 2007.

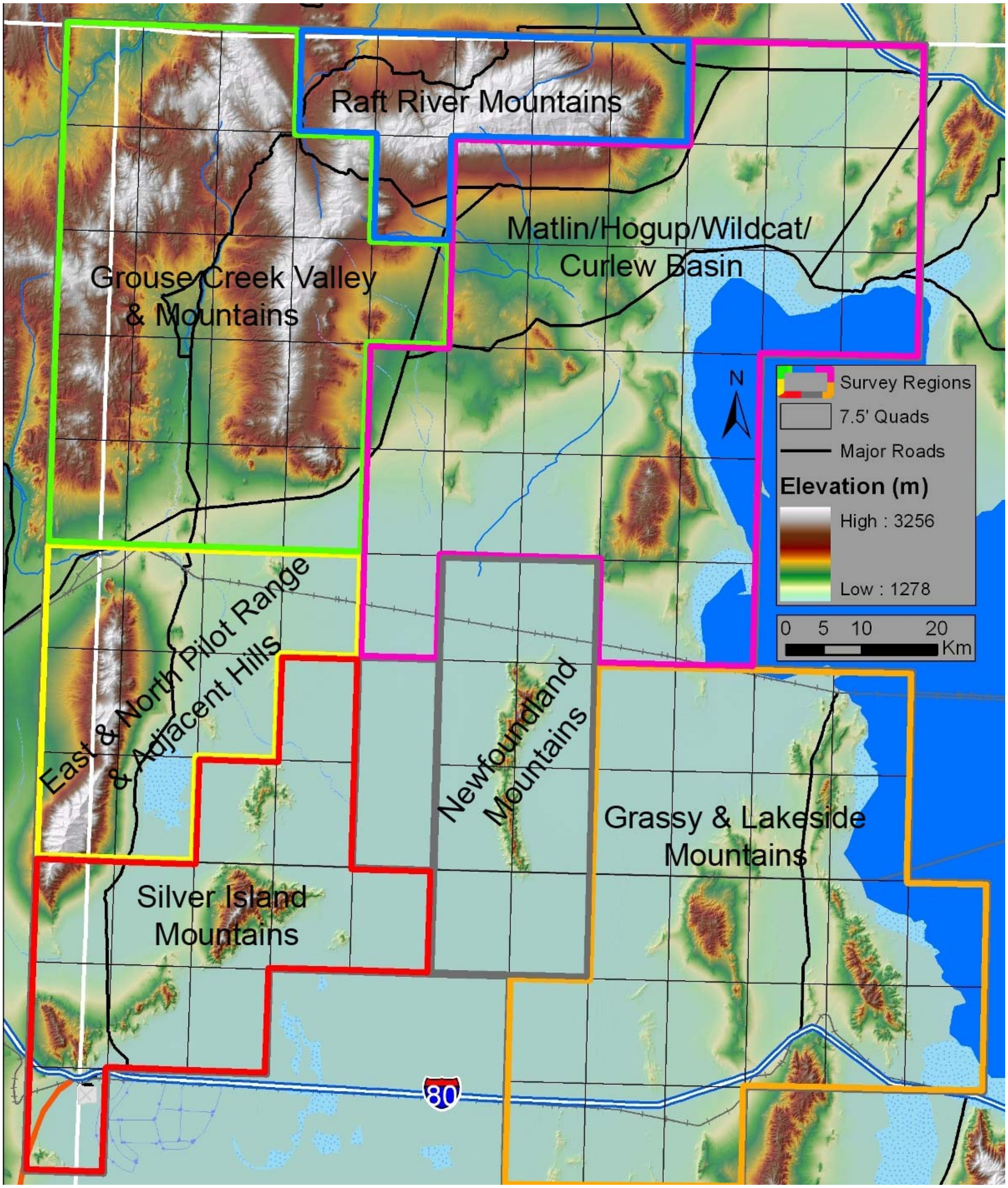

Figure 2. Raptor nest-survey regions in northwest Utah as defined by the distribution of 7.5′ topographic quads.

day hikes not requiring elaborate climbing gear, and with no violations of trespass laws. The study area boundary in Figure 1 roughly corresponds to the typical coverage area for the surveys beginning in 2001. Before 2001, coverage expanded considerably each year as we garnered resources to develop the larger survey and increased our familiarity with the area. Furthermore, coverage of the Grassy, Lakeside, Newfoundland, and Raft River mountains regions continued to improve through 2002. Additionally, resource limitations constrained the 2006 surveys to coverage of roughly 70% of the typical survey area, and implementation of a new quadrat-based survey design in 2007 (see Smith and Slater 2008 for details) constrained that year's effort to roughly 80% of the typical survey area, plus supplemental coverage of all other known Ferruginous and Swainson's Hawk nesting areas. Despite these variances, we feel strongly that, at least since 2001, the data we gathered each year yielded reliable estimates of study-area-wide population demographics.

FIELD METHODS

The senior author has served as the Principal Investigator for this study since its inception and has been involved in data collection at varying levels during all years of the study. Otherwise, annual survey teams typically consisted of three or four seasonal crewmembers and a HWI staff-level field coordinator (two individuals over the course of the study as represented here), supplemented at varying levels by efforts of other HWI staff and local volunteers.

Each year, concentrated survey work occurred throughout the period from 15 March through 15 July, except when hampered by inclement weather. This period effectively encompasses the majority of the nesting cycle of all focal species in this region (Haug et al. 1993, Preston and Beane 1993, Bechard and Schmutz 1995, England et al. 1997, Steenhof 1998, Kochert et al. 2002, White et al. 2002); however, additional visits extending into early August often were necessary to collect final data on late-nesting Swainson's Hawks and Burrowing Owls. Our objective was to visit each active nest at least three times during the season, first to document "activity status" (territory occupancy and egg laying), second to document hatching and initial brood size, and third to document "productivity" (number of successful pairs and fledgling production; Steenhof and Newton 2007).

Surveyors worked from 4WD vehicles constrained to established backcountry roads and on foot. Known nests and nesting territories were deemed inactive (i.e., non-breeding) if two extended observation periods separated by at least three weeks during the typical nest-building and incubation period for the species failed to reveal signs of recent activity (e.g., adults in courtship, exhibiting territorial defense behavior or nest building, fresh feces or nest material at the nest, or evidence of eggs or young). Three to five hour observation periods commonly are recommended to document territory occupancy of Peregrine Falcons (U.S. Fish and Wildlife Service 1984, Cade et al. 1996, R. V. Ward, Grand Canyon National Park, personal communication, F. Howe, UDWR, personal communication). Steenhof et al. (1999) employed two-hour observation periods during point surveys to document territory occupancy of Prairie Falcons in the Snake River region of Idaho. For other open-nest species such as the buteos, shorter observation periods more often are sufficient because it is possible to see directly into the nest or at least see adults sitting on the nest. Similarly, it usually is possible to confirm activity at Burrowing Owl colonies within a shorter period (e.g., ≤30 minutes) because actively nesting adults usually are quick to respond to intrusion by vocalizing or flying from the burrow (J. Parrish, UDWR, personal communication). Thus, to confirm inactivity at known territories where an incubating adult was not visible to ground-based observers, surveyors strived for a standard of observing for at least three hours per visit. For Burrowing Owls, we considered one-hour observation periods sufficient. Similarly, for nests where an incubating adult could be seen if present but the actual nest bowl was not visible, we adopted a standard of one-hour observation periods to confirm that nest building was not underway.

Otherwise, surveyors identified new nesting territories by searching suitable habitat with binoculars and spotting scopes for fecal deposits on cliffs, exposed nest structures on trees and shrubs, and adult birds. They located active nests primarily by following adult birds exhibiting territorial defense behavior (e.g., aggressive vocalizations and diving at intruders), carrying nest material or food, or swapping incubation/brooding duties with mates (Fuller and Mosher 1987). Direct observation of nests with fresh eggs or young also frequently resulted in confirmation of active status despite the apparent absence of adults (Steenhof and Newton 2007).

For most raptor species, it is critical that direct disturbance to the nest be severely restricted until chicks have hatched. Before this stage in the nesting cycle, close intrusions may cause abandonment by adults or exposure of eggs to excessive environmental stress (Fyfe and Olendorff 1976). For this reason, our surveyors restricted their activities to observation from a distance with binoculars and spotting scopes until adult activity patterns (e.g., food deliveries) or carefully controlled intrusions governed by appropriate seasonal timing (i.e., timing based on projections from previous nest studies as to when most nests typically hatch in the region) clearly indicated that the timing was appropriate for more intrusive investigations. Minimum observation distances during high-sensitivity periods conformed to disturbance-buffer guidelines established by the U.S. Fish and Wildlife Service (Romin and Muck 2002). More generally, surveyors always strived to record data and vacate active nest sites as quickly as possible to minimize disturbance. In addition to considerations of seasonal timing, our surveyors also strictly limited close intrusions on nests to times of day and weather conditions that did not expose eggs or young nestlings to excessive heat, cold, or moisture (Fyfe and Olendorff 1976).

Surveyors documented the geographic extent of their efforts and all nest locations on appropriate 7.5′ topographic maps. For each new active nest found, they recorded on a standardized nest-location data form, directions to the nest, a physical description of the nest, a description of the surrounding habitat, behavioral observations to verify status (active or inactive), productivity information when possible, diet/prey information when available, and approximate GPS coordinates (±15–20 m or better using handheld units such as the Garmin GPS II, 12XL, and GPS Map60CSx or, when available, a Trimble GeoExplorer). Digital photographs were taken of as many nest sites as possible, and subsequently were catalogued and directly tied to the project database to facilitate relocation in subsequent years. A nest-location form (Appendix A) was filled out for each new nest and a record of specific activity during each visit to a nest was recorded on a separate nest-history data form (Appendix B). Included on our standard nest-location and nest-history data forms were places to describe the habitats and human activities within a 1-km radius of each nest site.

Surveyors estimated nestling ages based on Moritsch (1983a, b; 1985), a similar unpublished photographic guide to aging Golden Eagles developed by raptor biologists at the USGS Snake River Field Station in Idaho (M. Kochert and K. Steenhof), and reasonable application of the Red-tailed Hawk and Ferruginous Hawk guides to aging similar Swainson's Hawks, albeit given the caveat that development of the latter species tends to proceed a bit quicker.

TERMINOLOGY

In reporting our nest activity, success, and productivity results, the following definitions apply:

Territory: clusters of nests with known species associations (i.e., have been confirmed as active nests during this or previous surveys) that are presumed to represent the unique nesting "territories" (actively defended or not) of specific breeding pairs based on spatial relationships and histories of non-overlapping (within years) use.

Occupied territory: breeding-age raptor persistently present during nesting season on known breeding territory, and/or courtship/territory defense observed.

Active territory (or nest start): incubation, nestling attendance, or fledging activities documented; declaration of active status presumes that eggs were laid.

Inactive territory: no evidence of nesting activity, persistent presence of breeding age raptor or courtship/territory defense behavior observed.

Successful nest: a nest that produced at least one nestling that reached ≥80% of the average fledgling age for the species (Steenhof and Newton 2007).

Fledglings per nest start: average number of nestlings raised to ≥80% of the average fledgling age for the species among all active nests.

Fledglings per successful nest: average number of nestlings raised to ≥80% of the average fledgling age for the species among nests that produced at least one such nestling.

DATA PREPARATION

Territory Mapping and Random Point Generation

For all raptor species except Burrowing Owls, we grouped nest sites into species-specific nesting territories based on known species associations, histories of nest use, field knowledge, and inspection of nest spacing and configuration. We excluded from further consideration all nests of uncertain species association and territories lacking at least one record of occupancy during the 1998–2007 survey period. Due to their semi-colonial nesting habits, for Burrowing Owls we uniquely treated every burrow location known to have been occupied sometime during the 1998–2007 survey period as an independent sample unit. These classification procedures produced 727 raptor territories containing 1,233 individual nesting sites. We used ArcMap 9.3 to create point, line, and minimum-convex-polygon features to delineate territories with 1, 2, and 3+ nests, respectively, and to facilitate determinations of average nest and territory spacings. To facilitate analyses of habitat selection, we also selected 727 random points from within the available study area (as delineated in Figure 1) to correspond to the 727 known raptor territories. We constrained selection of the random points to a minimum spacing of 1.0 km to correspond to the average nearest-neighbor distance of existing raptor territories (1.1 km) and to reduce autocorrelation among points.

Elevation Data

We used a 30-m digital elevation model (DEM) to determine elevation at nest sites, elevation variability (i.e., the standard deviation [SD] of DEM pixel values) within selected radii of territories, aspect at nest sites, and terrain ruggedness within nesting territories. We calculated terrain ruggedness using the ArcGIS Vector Ruggedness Measure arcscript, which incorporated measures of both slope and aspect to determine the ruggedness of the 24-pixel-square landscape (equivalent to a 150 x 150-m area) surrounding the 30-m pixel on which each nest resided (Sappington et al. 2007). We included this measure in an attempt to describe topography on a more localized scale to distinguish between nests located in relatively flat areas from those on cliffs, bluffs, etc.

Vegetation Data

To describe the habitat/vegetation characteristics of the study area and raptor territories, we created a 30-m-resolution map by merging Southwest ReGAP (USGS National Gap Analysis Program 2005) and Idaho GAP (Landscape Dynamics Lab 1999) coverage data. We reduced this dataset by merging similar habitat classes, particularly classes with low coverage (i.e., we combined aspen forest and woodland with aspen-mixed conifer forest and woodland complex; active and stabilized dune with barren lands; limber (*Pinus flexilis*)–bristlecone (*P. aristata*) pine woodland with mixed conifer forest and woodland and spruce (*Picea* spp.)–fir (*Abies* spp.) forest and woodland; alpine bedrock and scree with volcanic rock and cinder land; developed, medium-high intensity with developed, open space-low intensity; invasive annual and biennial forbland with invasive annual grassland and invasive perennial grassland; montane sagebrush steppe with montane-subalpine grassland; bigtooth maple (*Acer grandidentatum*) ravine woodland with chaparral, Gambel oak (*Quercus gambelii*)-mixed montane shrubland, and mountain mahogany (*Cercocarpus* spp.) woodland and shrubland; playa/wash with wash; riparian woodland with riparian woodland and shrubland; semi-desert grassland with semi-desert shrub steppe). The final map contained 22 coverage classes: agriculture, aspen mix, barren land, big sagebrush (*Artemisia tridentata*) shrub, big sagebrush/grass, cliff and canyon, conifer, disturbed, exposed rock, greasewood (*Sarcobatus vermiculatus*) flat, human developed, invasive grass/forbland, marsh, mixed sagebrush shrub, mixed salt desert scrub, montane sagebrush/grass, montane shrub/scrub, pinyon-juniper, playa/wash, riparian wood/shrub, semi-desert shrub/grass, and water.

Fire Data

We used an annual fire history database (1976–2007) provided by the BLM – SFO to assess fire occurrence and extent in relation to raptor nests within the study area.

Climate Data

For each nesting season of interest, we used monthly data from the western division of Utah provided by the National Climatic Data Center (NOAA 2008) to summarize climatic conditions during the nesting season (Mar–Jun) and winter (Nov–Feb) and year (Feb–Mar) preceding the nesting season. We examined the Palmer Drought Severity Index (PDSI), total precipitation, and average temperature as possible climate descriptors. Due to the high correlation (i.e., ≥0.70 Pearson correlation) between PDSI and precipitation during the previous year and nest period, we chose to use the more informative PDSI for all analyses involving climate data. We also obtained a GIS layer depicting long-term average (1971–2000) precipitation across the study area at a pixel resolution of 593 m (PRISM Climate Group 2008). This layer did not vary on an annual basis but allowed us to capture at least some sense of the general spatial variation in climate across the study area.

DATA ANALYSES

Description of the Study Area, Basic Territory and Nest Characteristics, and Demographic Trends

We used basic statistics and graphs to characterize the study area, basic climatic conditions, and fire occurrences in relationship to known nests, and to summarize information about nesting substrates, nest-site elevations, and nest distributions by landowner. We used a simple one-way ANOVA and Bonferroni post-hoc comparisons to analyze species-specific differences in nest-site elevations. We used the GIS to calculate species-specific, nearest-neighbor distances among nests within individual territories and among territory centers (i.e., the centroid of all nest locations belonging to a given territory).

To assess patterns of consistency in use of individual nests, we identified all nests that had been surveyed for at least five consecutive years during the study period and that had been active (eggs laid) at least once during that time. We summarized consecutive years of nest activity at individual nests, as well as the length of gaps between nest activity (i.e., the greatest number of years observed between two documented nest starts at the same nest).

We used basic statistics to describe densities of focal-species territories (i.e., occupied at least once during the survey period) by survey region and to highlight potential geographic trends in territory activity. For each focal-species nesting territory, we also summarized annual territory occupancy, territory activity, nest survival probabilities (*sensu* Shaffer 2004; discussed further below), and fledgling production per nest start. Due to limited sample sizes for most metrics in the earlier survey years, we report only values for 2001–2007. We also calculated only occupancy statistics for Burrowing Owls because our surveys did not provide adequate assessments of activity and productivity metrics.

Where possible, we estimated laying dates for the five primary, diurnal focal species by backdating from estimated nestling ages. We excluded records without specific, estimated nestling ages accurate to at least ±2–3 days and used the most advanced age estimates when age information was recorded during multiple visits. Based on averages or mid-points of ranges reported in the literature, we assigned incubation periods of 42 days for Golden Eagles (Kochert et al. 2002), 32 days for Ferruginous Hawks (Bechard and Schmutz 1995), 31 days for Red-tailed Hawks (Preston and Beane 1993), 34 days for Swainson's Hawks (England et al. 1997), and 33 days for Prairie Falcons (Steenhof 1998). We used a combination of initial simple linear regression analyses and stepwise multiple regression (forward and backward selection; *P* to enter or remove = 0.15) to assess the potential influences of year, nest-elevation, and seasonal and annual climatic variation on laying dates.

Habitat Characteristics of Raptor Territories

We used 2-km-radius buffers around point, line, or polygon representations of individual nesting territories to describe the vegetation and landscape characteristics associated with focal-species nesting areas at a spatial scale roughly corresponding to the typical home ranges of the relevant species, and used the resulting data to compare raptor nesting habitats (combined-species level) to the overall availability of habitats within the study area and to compare the nesting habitats of different raptor species at a common spatial scale. We used *t*-tests to compare the average elevation of individual nests within territories and random points, and to compare the average coverage of 22 habitat/vegetation variables within 2 km of territory centroids and random points. We used Canoco (v. 4.51; Biometrics-Plant Research International, Wageningen, Netherlands) to produce a canonical correspondence analysis (CCA) bi-plot of raptor species and vegetation variables measured within 2 km of raptor territories. CCA creates uncorrelated linear combinations of environmental variables (i.e., axes) that maximize the dispersion of species scores. Scores are the average or "optimum" values of the environmental variables measured for each species. The bi-plots simultaneously depict the relationship of multiple raptor species to individual habitat variables underlying the environmental axes produced by the CCA (ter Braak 1995).

Identification of Analytical Spatial Scales

We derived variables representing the vegetation and landscape characteristics around focal-species nesting territories at three spatial scales. We then used these variables in all subsequent modeling analyses designed to investigate the influences of habitat and climate on the nesting activity, success, and productivity of individual species. The three spatial scales reflected variants of the "home-range" scale of interest. The first suite of species-specific spatial scales that we examined was based on habitat data from our study area. The other two were based on literature reviews to identify average and upper-limit home-range sizes for each species, emphasizing data from the western U.S., Utah, and surrounding areas.

To develop the first suite of study-area-specific spatial scales for the six, primary focal species, we used a combination approach involving discriminant function analyses (using Systat 10; SPSS, Inc., Chicago, IL) and graphical assessments to determine at which of 10 spatial scales (0.5–5.0-km radii around territory centroids or random points, in increments of 0.5 km) differences in habitat coverage between raptor nesting territories and random points appeared most pronounced. For each spatial scale and species, we used an independent discriminant function analysis to assess the discriminatory abilities of the 22 habitat/vegetation variables measured around relevant nesting territories and an equal number of points randomly selected from among the 727 original random points generated for the study area as whole. We then examined post-hoc classification matrices to determine for each species which of the 10 spatial scales produced the greatest ability (i.e., highest classification accuracy) to distinguish nesting territories from random points based on habitat. Although variability in the actual magnitude of classification accuracies across spatial scales often was not pronounced, in all cases a clear peak extending across no more than one or two spatial scales was apparent (e.g., see Figure 3). To provide further insight at the level of individual habitat variables, we used graphical comparisons to examine variation in the average coverage of each habitat type around territories and comparable numbers of random points across the suite of spatial scales. Where apparent, these assessments identified the spatial scale(s) at which differences in coverage of individual habitat types between nesting territories and random points were maximized. We then compared plots for the full suite of habitat variables to identify common patterns of apparent selection tendency. In general, selection tendencies were either clearly apparent for only a few habitat types or there was a clear general tendency favoring a particular buffer scale, such that it was relatively easy to identify one or two spatial scales where such tendencies appeared most common across habitat types (e.g., see Figure 4). Finally, we combined insight derived from both approaches to select for each species the single spatial scale that appeared to illustrate the greatest differences between the habitats surrounding nesting areas and random points on the landscape. In general, the indicators from the two approaches tended to be similar and made for relatively easy selection of the final values (Table 1).

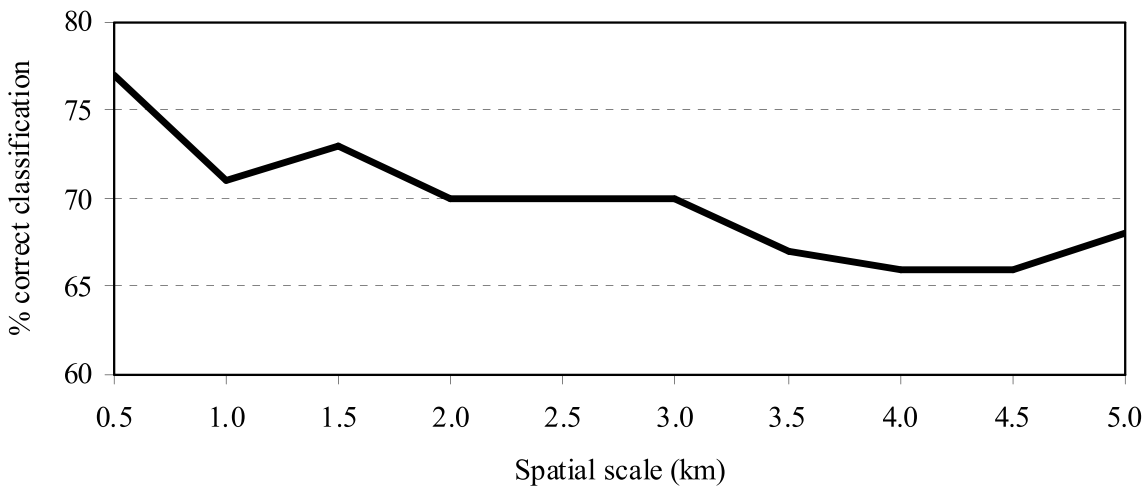

Figure 3. Example results of scale-specific discriminant function analyses used to assess the discriminatory abilities of 22 habitat/vegetation variables measured at different buffer-ring scales around relevant raptor nesting territories (727 multi-species territories) and an equal number of random points in northwest Utah. Y-axis values represent post-hoc classification accuracies for each spatial scale.

Table 1. Summary results comparing indicators of the most effective spatial scales (buffer radii from 0.5–5.0 km in 0.5-km increments) for discriminating habitat around raptor nesting territories in northwest Utah derived from two approaches: 1) scale-specific discriminant function analyses ("DF") used to discriminate habitat around raptor nesting territories and random points, and 2) graphics/visual-based assessments ("Visual") of differences between average coverage of individual habitat types around known nesting territories and random points evaluated at different spatial scales.

SPECIES	DF	VISUAL	SELECTED
Golden Eagle	0.5	0.5	**0.5**
Ferruginous Hawk	1.5	1.5	**1.5**
Red-tailed Hawk	1.5	0.5, 1.0	**1.0**
Swainson's Hawk	1.5	1.5	**1.5**
Prairie Falcon	2.0, 5.0	0.5, 2.0	**2.0**
Burrowing Owl	1.0, 2.5	1.0	**1.0**

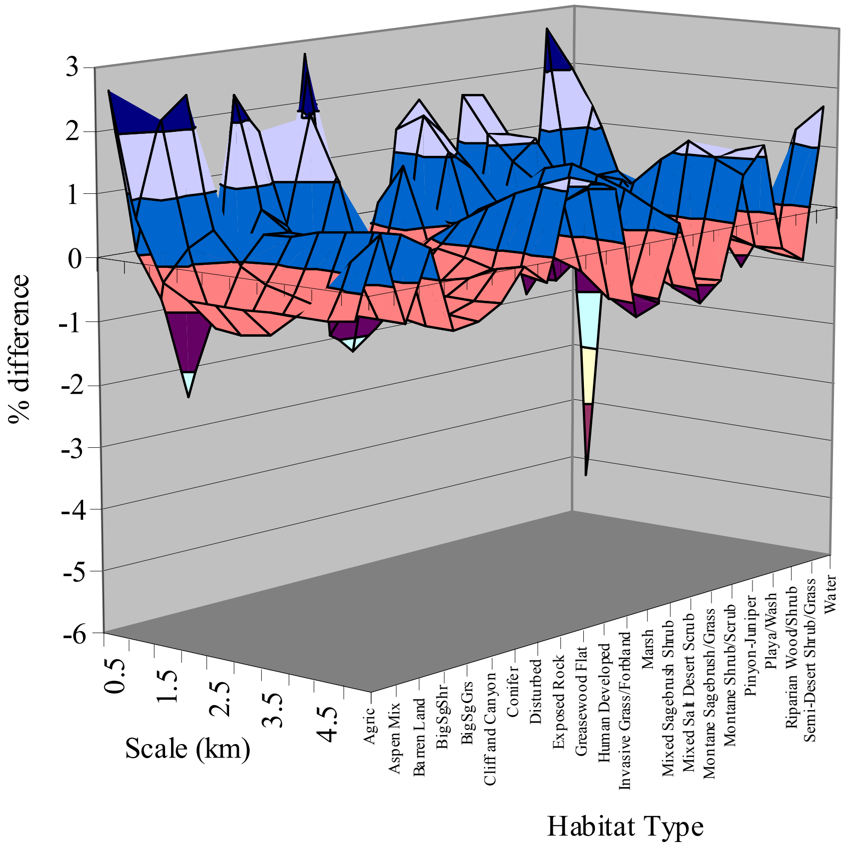

Figure 4. Example graphic to illustrate habitat selection tendencies of Golden Eagles at multiple buffer-ring spatial scales and across 22 vegetation/habitat-type variables type in northwest Utah. Values on the z-axis are the standardized (within habitat types) percentage differences between average coverage of a given habitat type within a given buffer ring size around known nesting territories and a corresponding number of random points.

The Golden Eagle literature suggested that birds breeding in the western U.S. exploit home ranges averaging 20–33 km² in size, depending on the study area, which is equivalent to a 2.5–3.2-km-radius circular home range (reviewed in Kochert et al. 2002). Researchers in north-central Utah (Smith and Murphy 1973) and southwestern Idaho (Marzluff et al. 1997a) both documented average breeding home ranges of 23 km² (2.7-km radius), but ranging as large as 83 km² (5.1-km radius). We therefore chose 3.0-km and 5.0-km radii to represent the spatial scale corresponding to average and upper-limit home range sizes in our analyses (Table 2).

Research from north-central Utah (Smith and Murphy 1973) and southwestern Idaho (McAnnis 1990) suggested that Ferruginous Hawk breeding home ranges average 6.0–7.6 km² in size (1.4–1.6 km radius) and range as high as 14.1 km² (2.1-km radius; McAnnis 1990); however, Leary et al. (1998) documented much larger average home ranges in Washington (90.3 km²; 5.4-km radius), likely due to relatively poor foraging habitat. Considering these studies, we chose 2.0 and 5.0-km radii as the scales of interest for our analyses (Table 2).

Table 2. Sizes of three spatial scales (radius of circular buffer) used to investigate relationships between raptor nesting ecology and habitat characteristics for six focal species in northwest Utah.

SPECIES	STUDY AREA[1]	AVG. HOME RANGE[2]	UPPER HOME RANGE[2]
Golden Eagle	0.5 km	3.0 km	5.0 km
Ferruginous Hawk	1.5 km	2.0 km	5.0 km
Red-tailed Hawk	1.0 km	1.0 km	2.0 km
Swainson's Hawk	1.5 km	3.0 km	5.0 km
Prairie Falcon	2.0 km	5.0 km	10.0 km
Burrowing Owl	1.0 km	0.5 km	1.5 km

[1] Derived based on evaluation of habitat around nesting territories and random points within the study area (see text for details).

[2] Based on values derived from review of literature on home range sizes estimated from other studies in western North America (see text for details).

We found relatively little information on Red-tailed Hawk home range sizes in the western U.S. The average nearest-neighbor distances between active nests in an intensively searched area of northern Utah was 2.8 km (Bosakowski et al. 1996). In two areas of Colorado, average nearest-neighbor distances were 0.7 and 2.2 km (McGovern and McNurney 1986). Home ranges in Oregon averaged 2.3 km² (0.9-km radius), but no range was given (Janes 1984). We chose 1.0 and 2.0-km radii as the scales of interest for our analyses (Table 2).

Breeding home ranges for the Swainson's Hawk are highly variable in the western U.S., averaging 6.2–40.4 km² (1.4–3.6 km-radius) depending on the study (reviewed in England et al. 1997). Smaller home ranges have been associated with alfalfa, fallow fields, and dry pasture habitats, whereas larger home ranges have been associated with less suitable crop types (e.g., grains and row crops). Home ranges in southeast Colorado averaged 21.3–27.3 km² (2.6–2.9-km radii; Andersen 1995). The largest documented home ranges, 76.6 and 87.2 km² (4.9 and 5.3-km radii), both were reported from central California (Babcock 1995, Estep 1989). We chose 3.0 and 5.0-km radii as the scales of interest for our analyses (Table 2).

Home range sizes of breeding Prairie Falcon also appear to be highly variable, with averages ranging from 59–315 km² (4.3–10.0-km radius) reported in the literature (reviewed in Steenhof 1998). Home range sizes in southwestern Idaho averaged 298 km² (9.7-km radius), with core use areas averaging 162 km² (7.2-km radius; Marzluff et al. 1997b). Home-range and core-area sizes in northeastern Wyoming averaged 112 km^2 (6.0-km radius) and 40 km^2 (3.6-km radius), respectively (Squires et al. 1993). Given this wide range in reported values, we chose 5.0 and 10-km radii as the scales of interest for our analyses (Table 2).

In southern Saskatchewan, adult Burrowing Owls spend most of their time within 0.3–0.6 km of the nest burrow (Haug and Oliphant 1990, Sissons et al. 2001, Gervais et al. 2003). In central California, the average maximum distance traveled from the nest was 1.3 km (Gervais et al. 2003). We chose 0.5 and 1.5-km radii as the scales of interest for our analyses (Table 2).

Modeling of Territory Activity, Probability of Nest Survival, and Productivity

We used AIC-based model-selection techniques to identify landscape, climate, and nest-site characteristics influential to annual territory activity (i.e., nest starts), proportional territory activity (i.e., the proportion of survey years a nest start was recorded in a territory), probability of nest survival, and productivity per successful nest. We excluded Burrowing Owls from the nest-survival and productivity analyses due to a lack of relevant data.

Response Variables.—Annual activity models included all territories with at least one nest start (eggs laid) during the survey years. Proportional activity models included all territories surveyed during ≥5 years and with at least one occupancy record (one or more breeding adults present) during the survey period. Typically, we classified territories as either "active" (eggs laid) or "inactive" (i.e., no nest start, but occupancy not precluded); however, due to the difficulty of distinguishing between occupancy and actual nest starts at Burrowing Owl burrows, we used occupancy as the response variable in both the annual and proportional activity models for this species. Because the logistic-exposure method of modeling nest survival (Schafer 2004) is dependent on observation intervals, we included in these analyses only nests with >1 observation during a given nesting period. We also excluded all failures from productivity models due to the potential survey bias they may introduce. That is, failure may occur at any time during the nesting season, so that the ability to detect failures is highly dependent on the timing of first nest visits. In contrast, for all nests, determination of the number of chicks produced occurs at a relatively consistent point in the nesting cycle (i.e., after chicks reach 80% of fledging age but before they actually fledge) and is thus largely unbiased by initial survey timing (i.e., unless initial surveys do not occur until very late in the nesting season after some nests may already have fledged). In contrast, our nest-survival modeling incorporated nest failures, but in such a way as to reduce the potential bias associated with survey timing (discussed further below).

Analyses of Nest Survival.—Because estimates of "apparent nest success" (i.e., the proportion of observed nests that are successful) often are positively biased by less than complete observation of all nests throughout the entire nesting period (Mayfield 1961, 1975), we used the "logistic-exposure" modeling technique (Shaffer 2004) to estimate nest survival and investigate relevant influences of landscape and climatic variables. Specifically, we produced multiple logistic regression models relating the binomial response variable, nest fate (0 = failed, 1 = successful), to landscape, climate, and nest-site variables based on a modified logit link function to account for variability in the lengths of nest-observation intervals (Shaffer 2004). The modified logit link function took the form $g(\theta)=\log_e(\theta^{1/t}/[1 - \theta^{1/t}])$, where θ is the interval survival rate and *t* is the interval length in days. This method treats observation intervals as sample units and assumes that survival and predictor variables are constant within intervals (T. Shaffer, USGS Northern Prairie Wildlife Research Center, personal communication).

Explanatory Variables.—Landscape variables included "vegetation factors" (VFs) and elevation variability (SD of DEM pixel values with proscribed territory or buffer areas) calculated at each spatial scale of interest for each focal species (Table 3). We derived scale-dependent VFs by using principal components analysis (PCA; Affifi and Clark 1997) to simplify the coverage datasets based on 22 original habitat/vegetation variables down to 6–10 orthogonal (i.e., uncorrelated) principal components (PCs). Such data reduction serves to reduce the potential risk of model overfitting (i.e., entering too many parameters relative to available sample sizes), removes potential issues concerning correlations among the original habitat variables, and helps simplify interpretation of model results. We used the PC coefficients and values of the original 22 vegetation variables measured at each scale to calculate species-, territory-, and scale-specific PC or VF scores, and examined variable loadings on each VF to help assign practical interpretations to those determined to be influential in subsequent model-building exercises (Affifi and Clark 1997).

Climate variables included average temperature and PDSI values for the year prior to the nesting season of interest, as well as for the previous winter (for models of annual activity) or nesting season itself (for models of nest survival and productivity). Because annual activity is simply a measure of nest starts, for these models we presumed it would be most important to model the temperature and moisture conditions prior to the start of the nesting season, whereas modeling conditions during the nesting season would be more relevant to analyses of nest survival and productivity. We did not include climate variables in models of proportional activity, because proportional activity is measured across years, precluding the use of annual climate variables.

Table 3. Groups of explanatory variables included in modeling analyses of annual nest activity (AA), proportional nest activity (PA), nest survival (NS), and nest productivity (NP). Retention in final models dependent on variable and model selection procedures outlined in the text.

GROUP	VARIABLES	AA	PA	NS	NP
Landscape	Vegetation factors (VFs[1]) and elevation variability (ElevSD) measured at study area, average home range, and upper home range scales	X	X	X	X
Climate	Previous year average temperature (PYTemp) and PDSI (PYPDSI)	X		X	X
	Previous winter (Nov-Feb) average temperature (PWTemp) and PDSI (PWPDSI)	X			
	Nesting season (Mar-Aug) average temperature (NSTemp) and PDSI (NSPDSI)			X	X
Nest Site	Number of nests in territory[2] (#Nests), elevation at nest (NSElev), and ruggedness (NSRugg) and average precipitation (NSPpt) at nest site	X	X	X	X
	Aspect at nest site (NSAsp[E, W, N, or S]; Golden Eagle and Prairie Falcon only)			X	X
	Nest height (NSHgt; Ferruginous Hawk and Swainson's Hawk only)			X	X
	Nest substrate (NSSub; Red-tailed Hawk only)			X	X

[1] Derived from principal components analyses that simplified 22 original habitat variables (see Table 3) into a lesser number of interpretable, orthogonal contrasts.

[2] Not applicable for Burrowing Owls.

Nest-site characteristics included the number of nests in a territory (except for Burrowing Owls for which we considered each occupied burrow an independent sample unit due to the difficulty of discerning territory dynamics for this colonial species), nest elevation, ruggedness near the nest, and the long-term average precipitation in the vicinity of the nest. For territories containing more than one nest, we averaged elevation, ruggedness, and precipitation values across all nests in the territory. For models of nest survival and productivity (in which specific nests, not territories, were the relevant sample unit), we included one additional variable for each species. For Golden Eagles and Prairie Falcons we added nest-site aspect (N, E, S, and W), because in all but one case (a single Golden Eagle tree nest) these two species nested on a cliffs or rocky outcrops, the aspect of which could greatly influence the thermal dynamics of the nest site. For Ferruginous Hawks and Swainson's Hawks, we added nest height because nests of these two species were found almost exclusively in junipers, a relatively short-statured tree/shrub. For Red-tailed Hawks, we included nest substrate because this was the only species that commonly used a wide variety of available substrates (e.g., cliffs/outcrops, a variety of coniferous and deciduous trees, and utility poles).

Model Building and Selection.—We used multiple logistic regression (Hosmer and Lemeshow 1989, Agresti 1990) to model annual activity (nest fate as the binomial response variable) and standard multiple regression to model proportional activity and productivity (both analyses conducted using SYSTAT 10.0). We used Program R (R Foundation for Statistical Computing, Vienna, Austria) to model nest survival with the logistic-exposure technique (Shaffer 2004). Using iterative, stepwise forward and backward addition of variables with P to enter and exit set at ≤ 0.15, we identified all significant annual activity, proportional activity, nest survival, and nest productivity models containing various combinations of landscape, climate, and/or nest-site variables (Table 3). We first built and analyzed separate models for each of the three variable groups (i.e., landscape, climate, and nest site) and for each of the three scale-specific groups of landscape variables. In each case, we identified the most robust and parsimonious model(s) based on the small-sample-size-correction form of Akaike's Information Criterion (AICc; Burnham and Anderson 2002). AICc is recommended for small sample sizes, but produces nearly identical results when sample sizes are large. For each species, we considered the top models (i.e., the most likely models, given the data under consideration) to be those with values of $\Delta AICc < 2$ (Burnham and Anderson 2002). For each species and response variable, we present the top models and their $\Delta AICc$ values, associated Akaike weights (w_i; i.e., the probability of a model given the data), and McFadden's ρ^2 (logistic and logistic-exposure models) or adjusted r^2 values (multiple regression models). Note that McFadden's ρ^2 values tend to be much lower than adjusted r^2 values due to the binary nature of the dependent variable in logistic regression, such that values between 0.2 and 0.4 may be considered indicators of satisfactory fit (Hensher and Johnson 1981). When a particular variable group was not represented in the top models, we also present the highest ranked (i.e., lowest ΔAICc) model from that group for reference. We interpreted the top models based on their underlying variables, relative weights, and explanatory ability.

RESULTS

STUDY AREA CHARACTERISTICS

We used GIS to describe the coverage of 22 GAP vegetation classes within the study area (Table 4). Various desert scrub/shrub/grass (39%) and big sagebrush/grass vegetation (31%) classes accounted for a combined 70% of the study area vegetation. Pinyon-juniper was the most common woodland vegetation cover (9.0%), while playa/wash (7.7%), invasive grass/forbland (6.4%), and agriculture (3.8%) also were relatively common, distinct vegetation or land-cover types. Half (11) of the individual vegetation classes were represented by <1% coverage.

Table 4. Ranked coverage of 22 vegetation/habitat types within the 9,087 km² northwest Utah study area).

VEGETATION TYPE	% COVER	VEGETATION TYPE	% COVER
Mixed salt desert scrub	22.2	Water	0.6
Big sagebrush shrub	15.8	Human developed	0.5
Greasewood flat	12.3	Barren land	0.4
Mixed sagebrush shrub	9.7	Riparian woodland/shrubland	0.4
Pinyon-juniper	9.0	Big sagebrush/grass	0.3
Playa/wash	7.7	Conifer	0.2
Invasive grass/forbland	6.4	Montane shrub/scrub	0.2
Montane sagebrush/grass	5.1	Aspen mix	0.1
Semi-desert shrub/grass	4.6	Disturbed	0.1
Agriculture	3.8	Marsh	0.1
Cliff and canyon	0.6	Exposed rock	<0.1

The study area experienced drought conditions from 1999 through 2004 and again beginning spring 2007 (Figure 5). Drought conditions and annual temperatures were most severe throughout 2003, but scorching conditions returned during late spring and summer 2007. In contrast, 1998 was the final year of a wet *El Nino* period that influenced conditions across much of western North America during most of the 1990s, and good winter snowpacks in 2004/2005 and 2005/2006 rendered 2005 a relatively mild and wet year overall following the preceding drought (Figure 5).

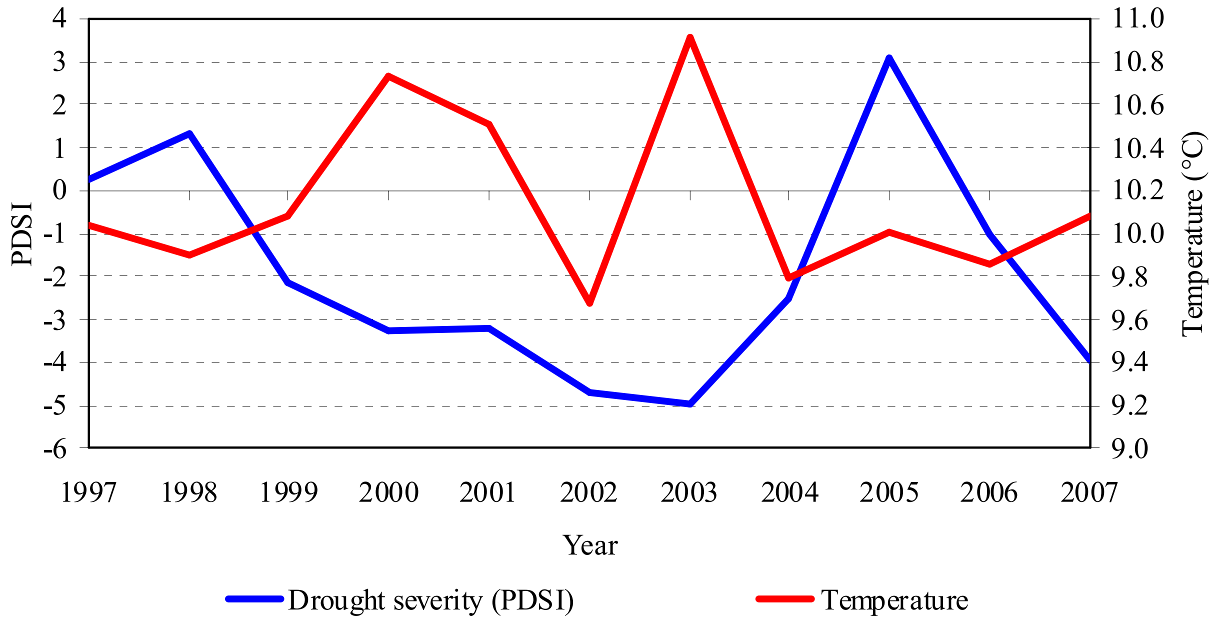

Figure 5. Average drought severity (PDSI; negative values indicate drought conditions) and temperatures in northwest Utah from 1997–2007.

No fires were documented in the study area between 1976 and 1996, and only a single small fire (3.8 km^2) was documented in 1997. None of the nests catalogued in our database (including many known from years prior to our study) are located in the area of the 1997 fire. Between 1998–2007, an average of 8.9 ± SE of 1.6 fires affected an average of 87.1 ± 32.5 km^2 of the study area per year; however, fire occurrence and coverage varied considerably across this period (Table 5, Figure 6). Fire was most prevalent in 1999 and 2000 and again in 2006 and 2007, whereas fires were least prevalent during the height of the drought from 2002–2004. In other words, wildfire was most prevalent following the wettest years of the study (1998 and 2005) when fuel loads were high and then drought conditions set in, and were comparatively low once extended drought had set in (2002–2004) because by then fuel loads had diminished considerably due to poor landscape productivity. At least 8 of 92 known raptor nests located in areas that burned during the study or were within a fire boundary were lost to fire during the study.

Table 5. Annual fire occurrence, areas affected, and raptor nests known prior to and destroyed by fire in the northwest Utah study area: 1998–2007.

YEAR	# OF FIRES	AREA BURNED (KM²)	NESTS IN BURNED AREA (# IN TREES)	NESTS DESTROYED
1998	3	12.9	0	0
1999	16	98.1	0	0
2000	11	152.3	2 (2)	0
2001	13	41.3	4 (1)	0
2002	1	0.8	0	0
2003	5	5.8	1 (1)	0
2004	7	5.4	5 (0)	0
2005	7	49.1	10 (1)	0
2006	13	197.6	20 (4)	3
2007	13	307.9	50 (8)	5 [1]
Total	89	871.2	92 (17)	8 [1]

[1] Figures are minimums because incomplete surveys in 2008 may have precluded the detection of some nest destruction by fires that occurred in 2007 but after surveys concluded.

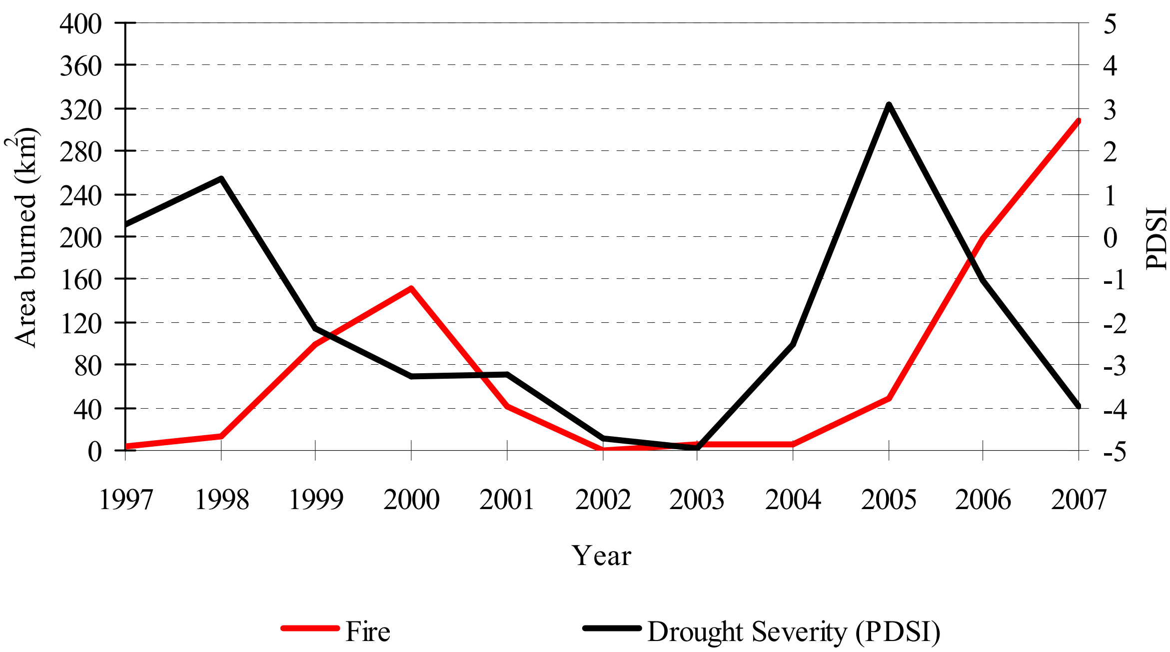

Figure 6. Average drought severity (PDSI; negative values indicate drought conditions) and area burned by wildfire in northwest Utah study area from 1997–2007.

NEST-SITE AND TERRITORY DYNAMICS

Distribution of Territories by Landowner

At the combined-species level, raptor nests were located on public (64%) and private (35%) land in proportion to their availability (Table 6). Only Red-tailed Hawk and Swainson's Hawk nests clearly were found more commonly on private lands than expected based on the relative extent of such lands.

Table 6. Distribution by landowner of all nests from raptor territories occupied at least once from 1998–2007 in the northwest Utah study area.

	SPECIES[1]								
LAND OWNER	GE	FH	RT	SW	PG	PR	BO	OTHER[2]	%
BLM	162	150	66	73	1	90	82	51	54.7
Military	4	0	0	0	0	2	0	1	0.6
State	31	10	12	6	1	18	19	6	8.4
USFS	3	0	7	1	0	1	0	3	1.2
Private	65	61	85	94	0	36	46	43	35.0
BLM/Private	0	1	0	0	0	0	0	0	0.1
State/Private	1	0	0	0	0	0	0	0	0.1
Total	266	222	170	174	2	147	147	104	100

[1] GE = Golden Eagle; FH = Ferruginous Hawk; RT = Red-tailed Hawk; SW = Swainson's Hawk; PG = Peregrine Falcon; PR = Prairie Falcon; and BO = Burrowing Owl.

[2] Other raptors were the Great Horned Owl (33), Long-eared Owl (33), American Kestrel (18), Barn Owl (9), Northern Harrier (4), Cooper's Hawk (3), Northern Goshawk (3), and Western Screech-Owl (1).

Nesting Substrates and Nest-Site Elevations

Of the 1,233 nests associated with the 727 raptor territories known to have been occupied at least once during the survey period, the vast majority occurred on cliffs or rocky outcrops (43%) or live, dead, or dying juniper trees (35%; Table 7). Another 12% were ground nests (all Burrowing Owl burrows except 2 Ferruginous Hawk ground nests) and 8% were located in various types of deciduous trees. More specifically, all but one Golden Eagle and all Prairie Falcon nests were on rocky substrates, most Ferruginous Hawk (84%) and Swainson's Hawk (86%) nests were in juniper trees, and Red-tailed Hawks made use of a wide variety of nest substrates, including a relatively high proportion of taller, often deciduous trees. Excluding Burrowing Owl burrows, 93% of the nests were stick nests, 5% were simple falcon scrapes, and the remaining 1% were miscellaneous types used by non-focal species (primarily cavities used by American Kestrels and reeds used by Northern Harriers).

ANOVA revealed significant variation (model $F_{5,\ 1120} = 46.2$, $P < 0.001$) in average nest-site elevations among the six, primary focal species (excludes Peregrine Falcons due to low sample size). Red-tailed Hawks averaged significantly higher nest-site elevations than all of the other focal species, whereas Burrowing Owls averaged significantly lower nest-site elevations than all other species (Bonferroni adjusted $P \leq 0.01$ in all cases; Table 8). The average elevation of Ferruginous Hawk nests was significantly higher than Burrowing Owls, but lower than all other species ($P \leq 0.05$). Golden Eagle, Swainson's Hawk, and Prairie Falcon average nest-site elevations did not differ significantly from one another (Table 8).

Table 7. Substrates of all nests from raptor territories occupied at least once from 1998–2007.

	Species[1]									
Substrate	GE	FH	RT	SW	PG	PR	BO	Other[2]	Total	%
Artificial Pole/Platform	0	2	1	0	0	0	0	0	3	0.2
Artificial Structure-Building	0	0	0	0	0	0	0	2	2	0.2
Artificial Structure-Utility Pole	0	2	5	4	0	0	0	0	11	0.9
Cliff/Outcrop	265	29	50	1	2	147	0	33	527	42.7
Ground	0	2	0	0	0	0	147	0	149	12.1
Tree-Conifer	0	0	5	2	0	0	0	3	10	0.8
Tree-Juniper (Live)	1	163	54	145	0	0	0	34	398	32.3
Tree-Juniper (Dead)	0	15	0	2	0	0	0	0	17	1.4
Tree-Juniper (Dying)	0	8	0	3	0	0	0	0	11	0.9
Tree-Aspen	0	0	9	0	0	0	0	2	11	0.9
Tree-Cottonwood	0	1	22	1	0	0	0	11	35	2.8
Tree-Unknown Poplar	0	0	13	2	0	0	0	6	21	1.7
Tree-Other Deciduous	0	0	8	12	0	0	0	9	29	2.4
Tree-Unknown	0	0	1	2	0	0	0	0	3	0.2
Other[3]	0	0	2	0	0	0	0	4	6	0.5
Total	266	222	170	174	2	147	147	104	1233	100

[1] GE = Golden Eagle; FH = Ferruginous Hawk; RT = Red-tailed Hawk; SW = Swainson's Hawk; PG = Peregrine Falcon; PR = Prairie Falcon; and BO = Burrowing Owl.

[2] Other raptors were the Great-horned Owl (33), Long-eared Owl (33), American Kestrel (18), Barn Owl (9), Northern Harrier (4), Cooper's Hawk (3), Northern Goshawk (3), and Western Screech Owl (1).

[3] Includes phragmites (3) and cattails (1) used by Northern Harriers, and mountain mahogany (2) used by Red-tailed Hawks.

Table 8. Analysis of variance (ANOVA) nest-site elevations for six focal raptor species and nests from territories occupied at least once from 1998–2007 in northwest Utah.

		Elevation (m)			
Species	# nests	Mean	SE	Range	Analysis[1]
Golden Eagle	274	1592.4	13.96	1290–2629	A
Ferruginous Hawk	222	1484.7	6.70	1301–1902	B
Red-tailed Hawk	176	1683.1	17.50	1302–2677	C
Swainson's Hawk	181	1582.5	8.89	1321–1818	A
Prairie Falcon	147	1540.6	16.59	1293–2225	A
Burrowing Owl	147	1420.5	7.80	1295–1674	D

[1] Species that do not share letters are significantly different from one another based on Bonferroni adjusted post-hoc comparisons ($P \leq 0.05$).

Red-tailed Hawk and Golden Eagle nests were spread across the broadest range of elevations (>1,300-m range) and were found at the highest elevations (>2,600 m). In contrast, Burrowing Owl nests were found across the narrowest range of elevations (379 m), followed by the Swainson's Hawk (479 m) and Ferruginous Hawk (601 m). Finally, Prairie Falcon nests were found across a more moderate range of elevations (932 m).

Use of Alternate Nest Sites

Based on nests and territories still extant after the 2007 survey year, Golden Eagle, Swainson's Hawk, and Prairie Falcon territories contained 1–6 nests, Ferruginous Hawk territories 1–17 nests, and Red-tailed Hawk territories 1–4 nests (Table 9). The two known Peregrine Falcon territories each contained a single eyrie (one location used only once), and for reasons of practical simplicity we considered all Burrowing Owl burrows as separate territories. The average distances between species-specific territory centers (i.e., the centroid of all nests in a given territory) ranged from 2.4–5.1 km for the six primary focal species (excludes Peregrine Falcon, with only 2 known, widely spaced territories; Table 9). Minimum spacing between territory centers suggests that all six focal species will tolerate intra-specific territory spacing of <1.0 km, although minimum spacing of <0.5 km occurred only for the Red-tailed Hawk (0.47 km), Swainson's Hawk (0.16 km), and Burrowing Owl (<0.01). Average intra-territory spacing of nests ranged from 0.3–0.6 km, within minimum spacing <20 m for all relevant species (Table 9). The very small minimum nest spacing reported for the Golden Eagle, Red-tailed Hawk, and Prairie Falcon was related to nests located on the same cliff face or outcrop.

Table 9. Species-specific descriptive statistics of nests per territory, territory spacing, and nest spacing within raptor nesting territories in the northwest Utah study area. The statistics include only territories occupied at least once from 1998–2007 and territories and nests still extant after the 2007 survey year.

		Nests per Territory			Territory Spacing (km)[1]			Nest Spacing (km)[2]			
Species	*n*	Mean	SE	Range	Mean	SE	Min.	*n*	Mean	SE	Min.
Golden Eagle	113	2.25	0.12	1–6	5.06	0.28	0.74	214	0.59	0.05	<0.01
Ferruginous Hawk	66	2.88	0.33	1–17	5.10	0.61	0.68	165	0.42	0.04	0.02
Red-tailed Hawk	102	1.37	0.07	1–4	3.83	0.35	0.47	67	0.49	0.08	<0.01
Swainson's Hawk	77	1.96	0.14	1–6	2.73	0.27	0.16	113	0.33	0.04	0.01
Peregrine Falcon	2	1.00	0.00	–	48.64	0.00	48.64	--	--	--	--
Prairie Falcon	88	1.53	0.10	1–6	4.75	0.41	0.84	77	0.46	0.07	<0.01
Burrowing Owl	132	1.00	0.00	–	2.43	0.35	<0.01	--	--	--	--

[1] Territory spacing was calculated from the mean center (centroid) of nests belonging to each territory.

[2] Nest spacing was measured between each nest from a multi-nest territory and its nearest neighbor.

Temporal and Spatial Patterns of Territory Activity

The maximum number of consecutive years an individual nest was active was 8 (out of 9 possible) for the Red-tailed Hawk (n = 36), 7 for the Golden Eagle (n = 110), 6 for the Prairie Falcon (n = 52), 5 for the Ferruginous Hawk (n = 55) and Swainson's Hawk (n = 47), 4 for the Burrowing Owl (n = 45), and 1 for the Peregrine Falcon (n = 2). Individual nests were used for at least two consecutive years at 45.5% of Golden Eagle nests, 41.8% of Ferruginous Hawk nests, 58.3% of Red-tailed Hawk nests, 36.2% of Swainson's Hawk nests, 40.4% of Prairie Falcon nests, and 37.8% of Burrowing Owl burrows. Considering gaps in nest activity, we documented a maximum of 6 years between nest starts at a given nest for the Golden Eagle (*n* = 50) and Red-tailed Hawk (*n* = 12), 5 years for the Swainson's Hawk (*n* = 14) and Prairie Falcon (*n* = 22), and 4 years for the Ferruginous Hawk (*n* = 14), Burrowing Owl (*n* = 12), and Peregrine Falcon (*n* = 1). Gaps between nest starts of three or more years occurred at 11–31% of focal species nests (Table 10).

Table 10. Percentage of nests experiencing various intervals between nest starts for six focal species in the northwest Utah study area from 1998–2007. Only nests surveyed consecutively for ≥5 years and active at least once during that period are represented.

		Years Between Nest Starts					
Species	*n*	0-1[1]	≥2	≥3	≥4	≥5	6
Golden Eagle	110	54.5	45.5	25.5	10.9	2.7	0.9
Ferruginous Hawk	55	74.5	25.5	10.9	3.6	0.0	0.0
Red-tailed Hawk	36	66.7	33.3	19.4	8.3	2.8	2.8
Swainson's Hawk	47	70.2	29.8	14.9	6.4	2.1	0.0
Prairie Falcon	52	57.7	42.3	30.8	17.3	7.7	0.0
Burrowing Owl	45	73.3	26.7	17.8	6.7	0.0	0.0
Total	345	64.1	35.9	20.9	9.3	2.6	0.6

[1] 0 represents nests with only a single nest start; 1 represents nests used only in consecutive years.

The estimated, study-area-wide density of all raptor territories occupied at least once during the survey period was 4.11 territories per 50 km² (all other subsequent values reported are per 50 km²). Regions that contained higher than average overall densities of raptor territories included the Grassy/Lakeside Mountains (5.9), Raft River Mountains (5.3), and Grouse Creek Valley and Mountains (4.5; Table 11). Similarly, Burrowing Owl (1.61), Prairie Falcon (1.23), Golden Eagle (1.19), and Ferruginous Hawk (0.75) territory densities were well above average in the Grassy/Lakeside Mountains region, whereas Red-tailed Hawk and Swainson's Hawk territory densities were relatively high in both the Raft River and Grouse Creek Valley and Mountains regions (Table 11). Golden Eagle and Prairie Falcon territories were also relatively common in the Newfoundland Mountains (no other focal species' territories occurred in this region) and the Silver Island Mountains.

We also used estimates of average proportional territory activity by region to further investigate potential regional patterns of territory distribution. Within the Raft River Mountains region, territory activity was 44% higher than the study-wide average at Swainson's Hawk territories, and 43% and 25% higher than average at Ferruginous Hawk and Red-tailed Hawk territories, respectively (Table 12). Similarly, Burrowing Owl activity was 36% higher and Prairie Falcon activity was 27% higher than average in the Grouse Creek Valley and Mountains Regions. Proportional activity was higher for Burrowing Owls (28%) and Golden Eagles (21%) in the E/N Pilot Range and Adjacent Hills, but lower for Prairie Falcons (-23%). Golden Eagles exhibited lower than average proportional activity in both the Silver Island Mountains (-26%) and Newfoundland Mountains (-23%). Similarly, territory activity in the Grassy/Lakeside Mountains region was 41% lower for Red-tailed Hawks, 35% lower for Burrowing Owls, and 24% lower for Ferruginous Hawk territories compared to the study-wide averages for these species. Overall, the results suggest a north-south decreasing trend in proportional territory activity (Table 12). Appendix C provides graphical illustrations of the densities of territories, weighted by proportional activity across survey years, for the six focal species and all raptor species combined.

Table 11. Regional densities (per 50 km² of area surveyed) of raptor territories occupied at least once from 1998–2007 in the northwest Utah study area.

Survey Region	Species[1] (# Territories)								
	GE (115)	FH (72)	RT (116)	SW (82)	PG (2)	PR (93)	BO (146)	Other[2] (100)	Total (727)
E/N Pilot Range and Adjacent Hills	0.50	0.37	0.37	0.31	0.06	0.56	1.25	0.44	3.87
Grassy/Lakeside Mountains	1.19	0.75	0.52	0.00	0.00	1.23	1.61	0.56	5.86
Grouse Creek Valley and Mountains	0.63	0.49	1.22	0.82	0.00	0.28	0.37	0.70	4.54
Matlin/Hogup/Wildcat/Curlew Basin	0.38	0.32	0.33	0.38	0.00	0.27	1.07	0.63	3.39
Newfoundland Mountains	1.14	0.00	0.00	0.00	0.00	1.14	0.00	0.16	2.44
Raft River Mountains	0.52	0.52	1.73	1.64	0.00	0.09	0.09	0.69	5.28
Silver Island Mountains	0.88	0.00	0.29	0.00	0.07	1.17	0.15	0.07	2.63
Average	0.65	0.41	0.66	0.46	0.01	0.53	0.83	0.57	4.11

[1] GE = Golden Eagle; FH = Ferruginous Hawk; RT = Red-tailed Hawk; SW = Swainson's Hawk; PG = Peregrine Falcon; PR = Prairie Falcon; and BO = Burrowing Owl.

[2] Other raptors were the Great Horned Owl (33), Long-eared Owl (30), American Kestrel (18), Barn Owl (8), Northern Harrier (4), Cooper's Hawk (3), Northern Goshawk (3), and Western Screech-Owl (1).

Table 12. Percent deviation from species-specific, study-wide averages of proportional territory activity (proportion of years territory was active, or occupied in the case of Burrowing Owls) within regions in the northwest Utah study area. Values were calculated from territories occupied at least once from 1998–2007 and surveyed a minimum of 5 years, and only species/region combinations represented by at least 5 territories are displayed.

Survey Region[2]	Species[1]					
	GE	FH	RT	SW	PR	BO
Number of Territories	*96*	*59*	*47*	*49*	*49*	*68*
Study-Area-Wide Average Proportional Activity Level (%)	*52*	*35*	*59*	*52*	*51*	*36*
Raft River Mountains	18.7	43.4	25.3	43.7	–	–
Matlin/Hogup/Wildcat/Curlew Basin	17.9	7.7	4.0	2.8	12.4	0.6
Grouse Creek Valley and Mountains	-2.7	17.3	12.2	-14.3	26.8	35.8
E/N Pilot Range and Adjacent Hills	21.1	–	–	–	-22.6	28.0
Newfoundland Mountains	-22.9	–	–	–	-15.4	–
Silver Island Mountains	-25.9	–	–	–	-18.5	–
Grassy/Lakeside Mountains	-8.2	-24.2	-41.4	–	5.1	-35.4

[1] GE = Golden Eagle; FH = Ferruginous Hawk; RT = Red-tailed Hawk; SW = Swainson's Hawk; PR = Prairie Falcon; and BO = Burrowing Owl.

[2] Regions are ordered from north-to-south, based on the mean center location of all nests within each region.

Annual territory occupancy generally was high for Golden Eagles (≥71%), Red-tailed Hawks (≥62%), Prairie Falcons (≥59%), and Swainson's Hawks (≥58%; Table 13, Figure 7). Golden Eagle territory occupancy was particularly steady across years, only varying between 71–80%. Ferruginous Hawk occupancy generally was lower (27–62%), more variable, and reached its lowest point in 2002. For Peregrine Falcons, the first active nest we discovered in the northern Pilot Range was active only one year, then was taken over by Prairie Falcons. We discovered the second active nest/territory in the hills near Wendover two years later and this location has been occupied by at least one adult every year since. Proportional Burrowing Owl occupancy generally declined through the survey years (Table 13, Figure 7), but this may be largely due to the burrow-centric rather than true territory-oriented approach we took for this species (see Discussion). The actual number of occupied burrows remained comparatively stable from 2001–2007, with highs of 44 in 2002 and 41 in 2005, and between 24–32 otherwise; however, the low numbers recorded in 2001 (26), 2006 (24), and 2007 (26) are almost certainly underestimates due to limited coverage in those years (68% of known burrows monitored in 2001, 78% in 2006, and 65% in 2007, compared to 96–100% from 2002–2005). Otherwise, most species exhibited an upward bump in occupancy in 2005 (Figure 7), the wettest year during the survey period (Figure 5).

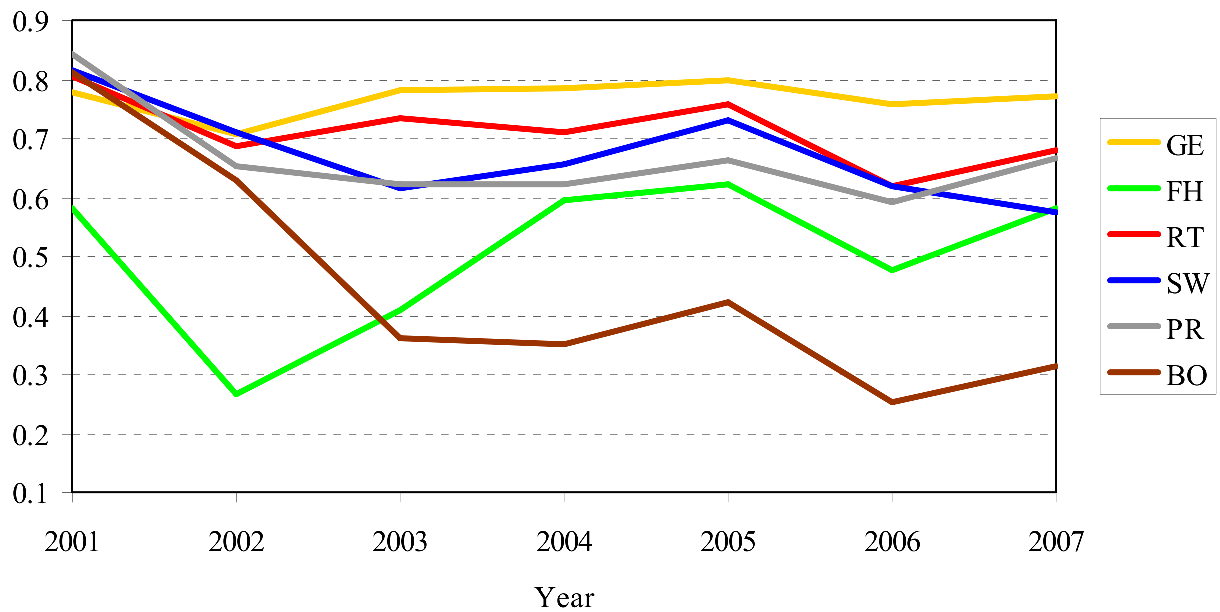

Figure 7. Annual variation in proportions of surveyed nesting territories that were occupied by six focal raptor species (GE = Golden Eagle; FH = Ferruginous Hawk; RT = Red-tailed Hawk; SW = Swainson's Hawk; PR = Prairie Falcon; and BO = Burrowing Owl) in northwest Utah from 2001–2007.

As with occupancy, annual activity values generally were higher at Red-tailed Hawk (47–67%), Golden Eagle (43–68%), Swainson's Hawk (42–71%), and Prairie Falcon (45–55%) territories compared to Ferruginous Hawk (29–46%) territories (Table 13, Figure 8). Similar to the pattern of occupancy, Ferruginous Hawk activity was low from 2002–2003, but rose steadily again across all remaining years. Golden Eagle territory activity was more variable than occupancy and showed an overall increasing trend from 2001–2007 with a peak in 2006. Red-tailed Hawk territory activity was again generally high and showed a slight declining trend through the study, but was more variable from year to year than occupancy. Swainson's Hawk and Prairie Falcon territory activity was mostly slightly lower but generally similar to those of territory occupancy (compare Figures 7 and 8). Golden Eagles, Swainson's

Hawks, and Prairie Falcons exhibited similar temporary declines in territory activity in 2003 (Figure 8), the year of peak drought (Figure 5). The Wendover Peregrine Falcon eyrie, although occupied every year from 2001–2007, was active and successful only three times: in 2001, the discovery year; in 2003, the peak drought year; and in 2007, when the summer turned scorching again after a respite in 2005/2006. In part due to a less-than-ideal monitoring effort, however, the activity status of the eyrie was left somewhat uncertain in 2006, with only a single adult and no fledglings ever seen, but failure a possibility.

Table 13. Annual territory occupancy, territory activity, nest survival, and fledglings per nest start in the northwest Utah study area from 2001–2007. Only territories and nests belonging to territories occupied at least once from 1998–2007 were included in the calculations.

		Species[1]					
Metric	Year	GE	FH	RT	SW	PR	BO
% Territories Occupied	2001	78 (77)	58 (31)	80 (41)	82 (38)	84 (38)	81 (32)
(# surveyed)	2002	71 (96)	27 (60)	69 (51)	71 (45)	65 (46)	63 (70)
	2003	78 (100)	41 (59)	74 (68)	62 (52)	62 (58)	36 (72)
	2004	79 (107)	60 (57)	71 (69)	66 (58)	62 (66)	35 (91)
	2005	80 (109)	62 (58)	76 (83)	73 (67)	66 (71)	42 (97)
	2006	76 (87)	48 (65)	62 (55)	62 (50)	59 (61)	25 (95)
	2007	77 (87)	58 (67)	68 (72)	58 (66)	67 (75)	31 (83)
% Territories Active	2001	43 (77)	42 (31)	54 (41)	71 (38)	55 (38)	--
(# surveyed)	2002	53 (96)	20 (60)	55 (51)	64 (45)	54 (46)	--
	2003	46 (100)	29 (59)	66 (68)	44 (52)	45 (58)	--
	2004	52 (107)	35 (57)	51 (69)	53 (58)	48 (66)	--
	2005	57 (109)	40 (58)	67 (83)	55 (67)	55 (71)	--
	2006	68 (87)	42 (65)	47 (55)	44 (50)	51 (61)	--
	2007	57 (87)	46 (67)	53 (72)	42 (66)	53 (75)	--
Mean Probability of Nest	2001	52 (6)	27 (19)	78 (9)	59 (10)	19 (8)	--
Survival	2002	66 (13)	49 (54)	77 (41)	84 (31)	55 (37)	--
(# of survival intervals)[2]	2003	80 (17)	46 (56)	89 (85)	86 (46)	95 (31)	--
	2004	75 (38)	70 (74)	92 (74)	80 (49)	83 (31)	--
	2005	85 (39)	87 (105)	90 (106)	88 (75)	87 (38)	--
	2006	95 (23)	94 (36)	87 (15)	79 (13)	100 (7)	--
	2007	87 (37)	86 (64)	83 (34)	44 (30)	86 (33)	--
Fledglings per Nest Start	2001	0.39 (33)	1.54 (13)	1.14 (22)	0.26 (27)	0.71 (21)	--
(# of nest starts)	2002	0.45 (51)	1.33 (12)	1.29 (28)	0.48 (29)	1.08 (25)	--
	2003	0.57 (46)	2.12 (17)	1.93 (45)	1.22 (23)	2.04 (26)	--
	2004	0.75 (56)	1.40 (20)	1.91 (35)	1.29 (31)	1.66 (32)	--
	2005	1.08 (62)	2.30 (23)	1.84 (56)	1.81 (37)	2.08 (39)	--
	2006	0.88 (59)	2.15 (27)	1.31 (26)	1.73 (22)	2.06 (31)	--
	2007	0.68 (50)	1.39 (31)	1.08 (38)	0.93 (28)	1.65 (40)	--

[1] GE = Golden Eagle; FH = Ferruginous Hawk; RT = Red-tailed Hawk; SW = Swainson's Hawk; PR = Prairie Falcon; and BO = Burrowing Owl.

[2] Based on methods of Schafer (2004).

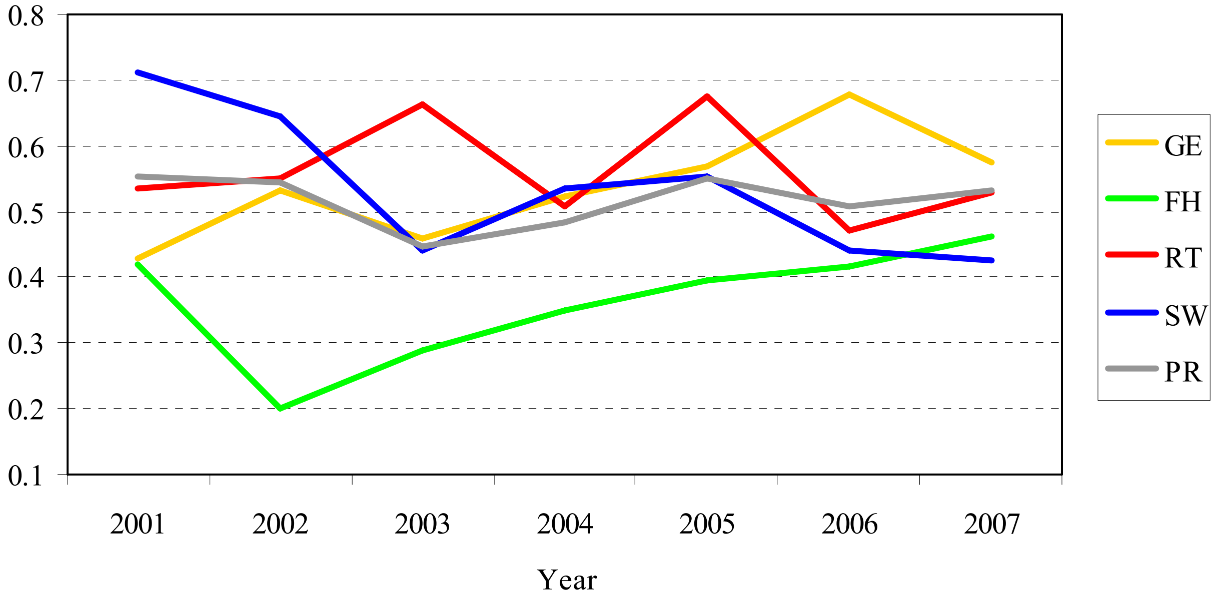

Figure 8. Annual variation in proportions of surveyed nesting territories that supported active nests of five focal raptor species (GE = Golden Eagle; FH = Ferruginous Hawk; RT = Red-tailed Hawk; SW = Swainson's Hawk; PR = Prairie Falcon) in northwest Utah from 2001–2007.

Nest Success and Productivity

For most species, the estimated probabilities of nest survival were noticeably lower in 2001 than in other years (Table 13, Figure 9). From there, the nest survival estimates for Ferruginous Hawks suggested a strong increasing trend through 2006, then a slight drop in 2007. Golden Eagle nest-survival estimates followed a similar pattern except for showing a slight decline between 2003 and 2004 instead of between 2002 and 2003. The pattern for Prairie Falcons was again similar overall, but with the survival estimate for 2003 nearly as high as for 2006. In contrast, Red-tailed Hawk nest survival remained comparatively high and stable (77–92%) through the study, and Swainson's Hawk nest survival remained comparatively high (79–88%) and stable from 2002–2006, but declined dramatically in 2007 to 44% (Figure 9).

Excluding the Red-tailed Hawk, the number of fledglings produced per nest start peaked in 2005 during the wettest year of the study and was only slightly lower in 2006 for all five primary, diurnal focal species (Table 13, Figure 10). Golden Eagles and Swainson's Hawks showed strong increasing trends in their productivity per nest start from 2001–2005. In contrast, Ferruginous Hawk and Prairie Falcon productivity was only slightly lower in 2003 during the peak drought year than during the wetter years of 2005 and 2006, and Red-tailed Hawk productivity was highest in 2003 and declined thereafter (Figure 10). Here it is important to consider that the productivity values for 2003 relate to 30–50% fewer active nests than in 2005, depending on the species. In other words, high productivity values in 2003 reflect few nests doing well, whereas high productivity in 2005 reflects many more nests doing well. Productivity at the single Wendover Peregrine Falcon eyrie followed a slightly different pattern, with three fledglings produced the first year (2001) but only two in 2003 and 2007.

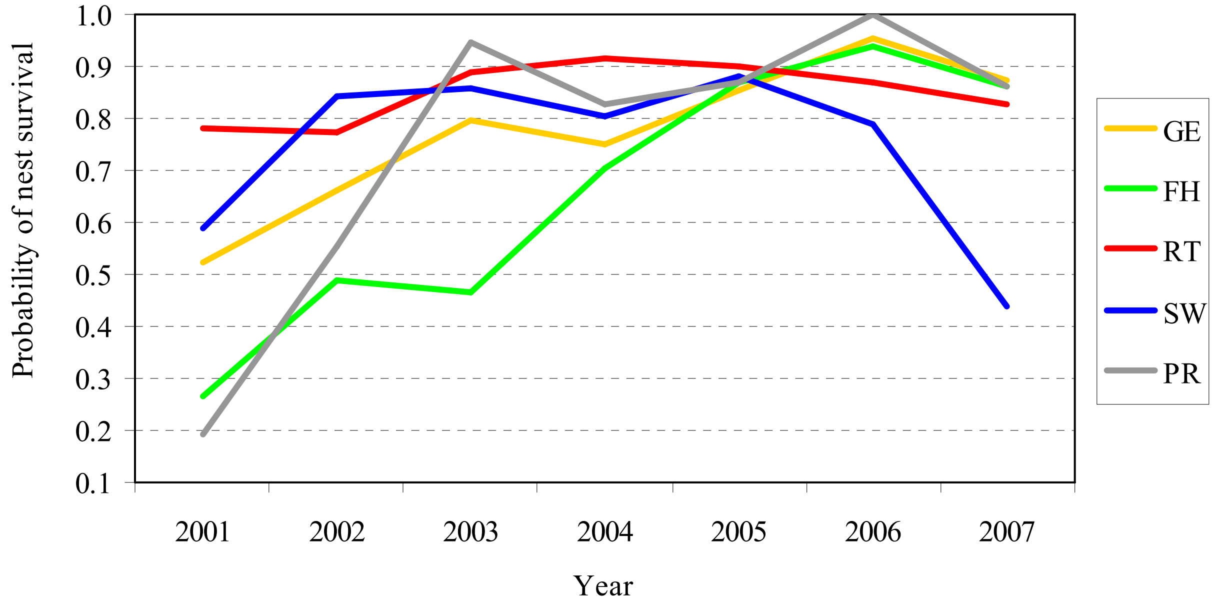

Figure 9. Annual variation in nest survival for five focal raptor species (GE = Golden Eagle; FH = Ferruginous Hawk; RT = Red-tailed Hawk; SW = Swainson's Hawk; PR = Prairie Falcon) in northwest Utah from 2001–2007.

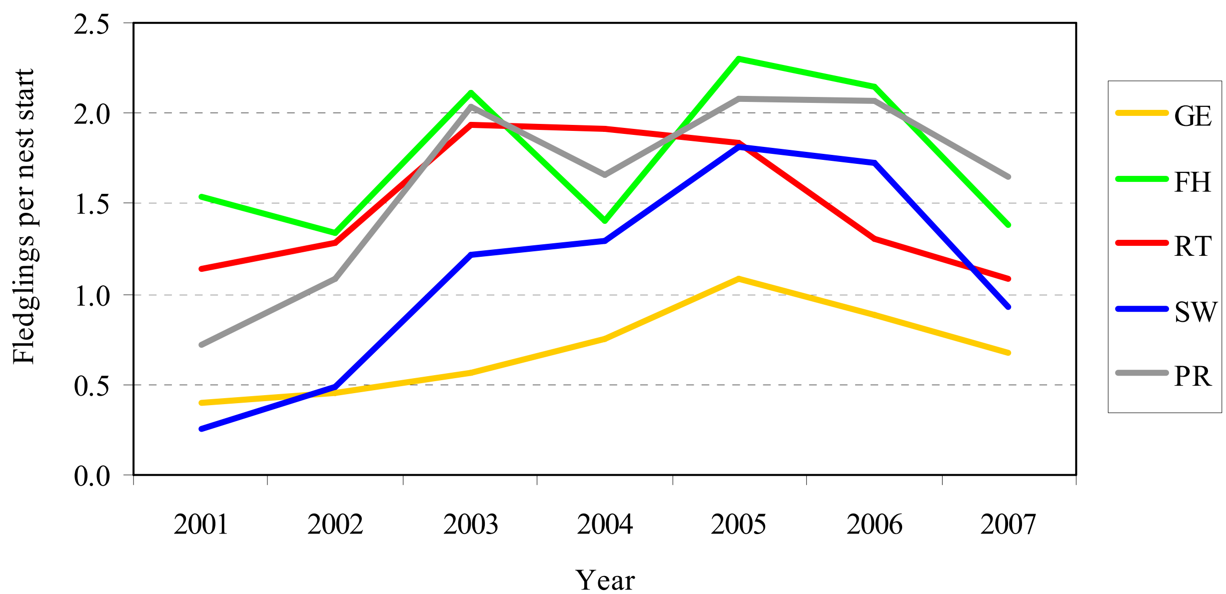

Figure 10. Annual variation in nest productivity for five focal raptor species (GE = Golden Eagle; FH = Ferruginous Hawk; RT = Red-tailed Hawk; SW = Swainson's Hawk; PR = Prairie Falcon) in northwest Utah from 2001–2007.

Nesting Phenology

We report laying dates for five focal species (excludes Peregrine Falcons and Burrowing Owls) for the years 2001–2007 (Table 14). Overall, laying dates averaged later in 2001 and 2002, earlier from 2003–2006, and moderate in 2007 (Figure 11). For Ferruginous Hawks, Golden Eagles, and Prairie Falcons, variability in laying dates (as reflected in standard deviations; Table 14) tended to be higher in 2001/2002 and 2007 when the dates averaged later. This pattern did not apply to Red-tailed Hawks, however, and Swainson's Hawks tended to show the opposite pattern with variability highest from 2003–2005 when the average dates were earliest.

Graphical inspection of the overall standardized laying dates of the five focal species suggested that, in general, egg laying tended to occur earlier in later years and in years with greater nesting season precipitation (Figure 12). However, neither simple, univariate linear regressions nor integrated multiple regression models suggested that year, nest-elevation, or climate variables explained statistically significant ($P > 0.05$) components of variation in laying dates for Ferruginous and Swainson's Hawks. In contrast, univariate regression indicated a highly significant ($P < 0.001$) relationship between Golden Eagle laying dates and average site precipitation or year; i.e., laying dates averaged 1 day later for every 2.6 cm increase in average precipitation received at a nest site or 1 day earlier for every 0.8 survey-years passed. No other predictors were deemed significant according to univariate regressions; however, the final multiple-regression model also included average winter temperature as a marginally significant ($P = 0.046$) predictor (i.e., colder winters correlate with later laying), but with the combination still accounting for a relatively low 9.0% of the total variance in the data (Table 15). For Red-tailed Hawks, initial univariate regressions revealed nest elevation and year as the best individual predictors of laying dates (PXX), suggesting laying was delayed 1 day for every 71 m gain in elevation or every 0.7 survey-years passed. Again, however, the final multiple-regression model included two other highly significant predictors, with the overall model accounting for a relatively high 18% of the variance in this dataset (Table 15). Overall, this model suggested that laying generally occurred earlier during less drought-stricken nesting seasons and in later years, but tended to be delayed following wetter winters and at higher elevation. For Prairie Falcons, average site precipitation ranked as the only individual significant predictor (no multiple-regression models were identified), suggesting average laying date was 1 day later for every 5.1 cm increase in average site precipitation. This relationship was similar to that observed for Golden Eagles (i.e., later laying associated with generally wetter sites), but the model only accounted for 2.9% of the total variance in the data (Table 15).

Table 14. Annual and overall-average laying dates of five focal raptor species in northwest Utah from 2001–2007.

	Ferruginous Hawk			Golden Eagle			Prairie Falcon			Red-tailed Hawk			Swainson's Hawk		
Year	Date	SD	*n*	Date	SD	*n*	Date	SD	*n*	Date	SD	*n*	Date	SD	*n*
2001	Apr 14	10.4	12	Mar 10	13.0	10	Apr 18	16.2	6	Apr 18	6.8	14	May 8	3.0	13
2002	Apr 18	4.7	11	Mar 6	12.4	25	Apr 15	10.4	18	Apr 19	8.8	22	May 12	6.1	21
2003	Apr 9	4.8	12	Mar 3	9.0	23	Apr 13	9.0	21	Apr 9	9.0	41	May 6	13.2	19
2004	Apr 14	7.3	17	Mar 2	9.2	39	Apr 14	5.1	21	Apr 9	9.1	30	May 6	15.8	22
2005	Apr 11	9.9	20	Feb 27	10.7	50	Apr 13	9.2	33	Apr 7	11.8	53	May 6	10.0	35
2006	Apr 13	8.3	22	Feb 26	13.2	36	Apr 10	7.8	17	Apr 9	14.8	11	May 7	8.2	18
2007	Apr 11	11.3	22	Mar 1	16.9	39	Apr 14	10.2	22	Apr 12	11.5	21	May 10	9.5	19
All	Apr 13	8.9	116	Mar 2	12.8	222	Apr 14	9.2	138	Apr 11	10.9	192	May 8	10.5	147

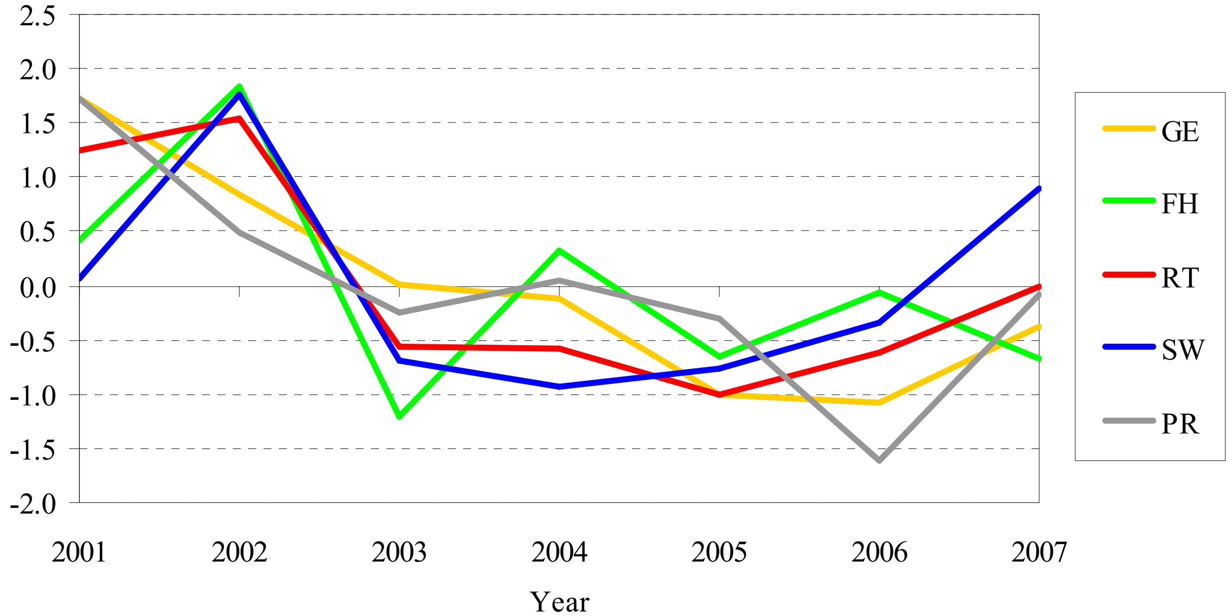

Figure 11. Average standardized laying dates of five focal raptor species (GE = Golden Eagle; FH = Ferruginous Hawk; RT = Red-tailed Hawk; SW = Swainson's Hawk; PR = Prairie Falcon) in northwest Utah from 2001–2007.

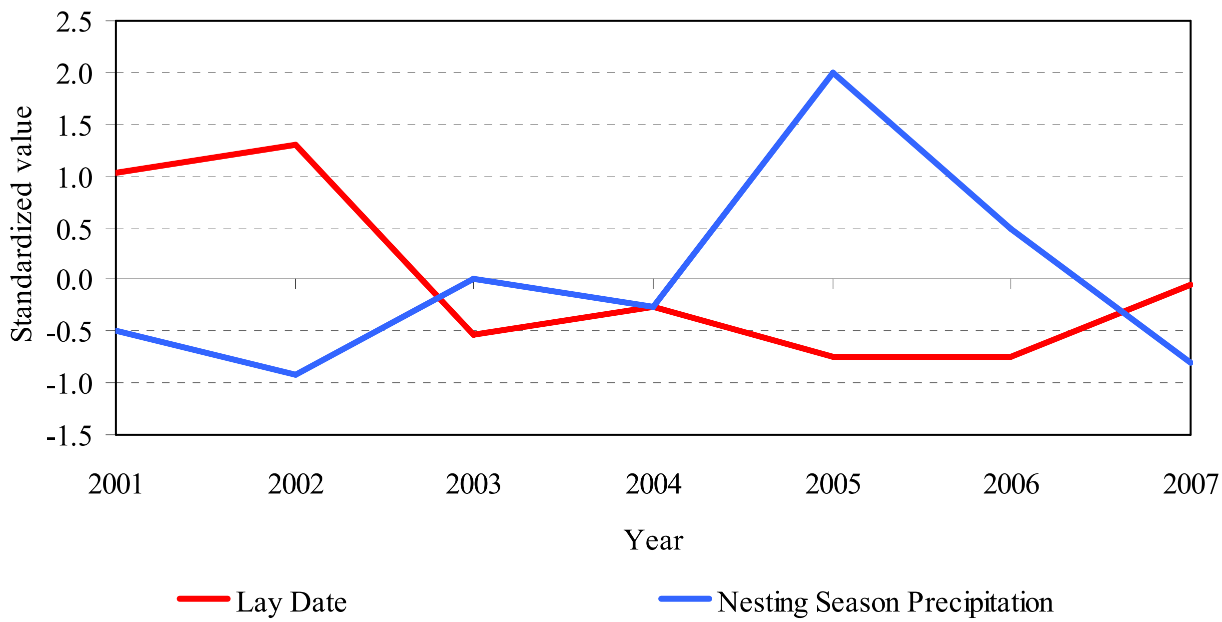

Figure 12. Variation in standardized, average laying dates for five focal raptor species in relation to standardized (for ease of display) nesting-season (March–June) precipitation in northwest Utah from 2001–2007.

Table 15. Results of species-specific, stepwise multiple regression modeling relating laying date to year, nest elevation, and climate variables for five focal raptor species in northwest Utah. No significant models were evident for Ferruginous and Swainson's Hawks.

SPECIES	VARIABLE	COEFFICIENT	SE	*P*	ADJ. R^2
Golden Eagle	Constant	2526.00	934.86	0.007	0.090
	Year	-1.22	0.47	0.009	
	Avg. Site Precipitation (cm)	0.36	0.10	<0.001	
	Avg. Winter Temperature (°C)	-0.79	0.39	0.046	
Red-tailed Hawk	Constant	4541.02	1139.98	<0.001	0.175
	Year	-2.23	0.57	<0.001	
	Nest Elevation (m)	0.014	0.003	<0.001	
	Nesting Season PDSI[1]	-3.61	0.88	<0.001	
	Winter Season PDSI	4.77	1.26	<0.001	
Prairie Falcon	Constant	98.51	2.56	<0.001	0.029
	Avg. Site Precipitation (cm)	0.19	0.09	0.025	

[1] PDSI = Palmer Drought Severity Index.

HABITAT CHARACTERISTICS OF RAPTOR TERRITORIES

A comparison of the landscape and vegetation features measured at and within a 2-km radius of 727 raptor territories and an equal number of random points suggested that nests from raptor territories tended to be located at higher elevations (1,568 m vs. 1,529 m) and in areas of greater elevation variability (SD = 58.5 vs. 50.4) than random points (Table 16). Raptor territories also included higher average coverage of agriculture (6.7% vs. 4.0%), aspen mix (0.14% vs. 0.06%), big sagebrush shrub (20.4% vs. 17.6%), riparian woodland/shrubland (0.57% vs. 0.38%), and semi-desert shrub/grass (5.8% vs. 4.8%), but less coverage of greasewood flats (7.2% vs. 11.9%), marsh (0.08% vs. 0.16%) and playa/wash (2.0% vs. 3.9%) habitats than are available within the study area as a whole (Table 16).

The ordination of raptor species based on vegetation variables measured within 2 km of territories revealed apparent habitat preferences of individual species. Golden Eagle and Prairie Falcon territories were similar to one another and contained more cliff and canyon, barren land, playa/wash, and semi-desert shrub/grass relative to other raptor species (Figure 13). Burrowing Owl territories were associated with more invasive grass/forbland and mixed salt desert scrub. Ferruginous Hawk territories, and to a lesser degree, Long-eared Owl territories, contained more agriculture, invasive grass/forbland, and big sagebrush shrub. Swainson's Hawk territories were associated with more big sagebrush shrub and agriculture. American Kestrel and Red-tailed Hawk territories both contained more pinyon-juniper and montane sagebrush/grass, and Red-tailed Hawk territories also contained more riparian woodland/shrubland and human development. Similarly, Great Horned Owl territories were associated with more riparian woodland/shrubland and human development (Figure 13).

Table 16. Univariate comparisons (*t*-tests) of landscape and vegetation variables at and within 2 km of raptor territories (*n* = 727) occupied at least once from 1998–2007 and an equal number of random points within northwest Utah.

	Raptor Territories		Random Points		
Variable[1]	Mean	SE	Mean	SE	*P*
Elevation (m)	1,568	7.83	1,529	8.49	0.001
Elevation variability (SD)	58.6	1.5	50.4	1.5	0.000
Agriculture	6.65	0.61	3.99	0.50	0.001
Aspen mix	0.14	0.03	0.06	0.02	0.030
Barren land	0.52	0.10	0.42	0.10	0.482
Big sagebrush/grass	0.37	0.05	0.33	0.04	0.539
Big sagebrush shrub	20.37	0.85	17.56	0.79	0.016
Cliff and Canyon	0.60	0.10	0.52	0.07	0.467
Conifer	0.16	0.06	0.13	0.07	0.792
Disturbed	0.03	0.01	0.02	0.01	0.414
Exposed rock	0.01	0.00	0.00	0.00	0.019
Greasewood flat	7.23	0.45	11.85	0.68	0.000
Human developed	0.31	0.04	0.48	0.12	0.168
Invasive grass/forbland	7.05	0.47	6.71	0.50	0.625
Marsh	0.08	0.01	0.16	0.04	0.041
Mixed sagebrush shrub	12.02	0.58	11.99	0.63	0.977
Mixed salt desert scrub	22.42	0.94	23.30	0.94	0.511
Montane sagebrush/grass	4.84	0.61	3.84	0.51	0.205
Montane shrub/scrub	0.28	0.05	0.23	0.06	0.493
Pinyon-juniper	8.33	0.56	9.05	0.67	0.407
Playa/wash	1.98	0.27	3.89	0.40	0.000
Riparian woodland/shrubland	0.57	0.07	0.38	0.06	0.043
Semi-desert shrub/grass	5.81	0.28	4.77	0.26	0.007
Water	0.24	0.08	0.33	0.11	0.547

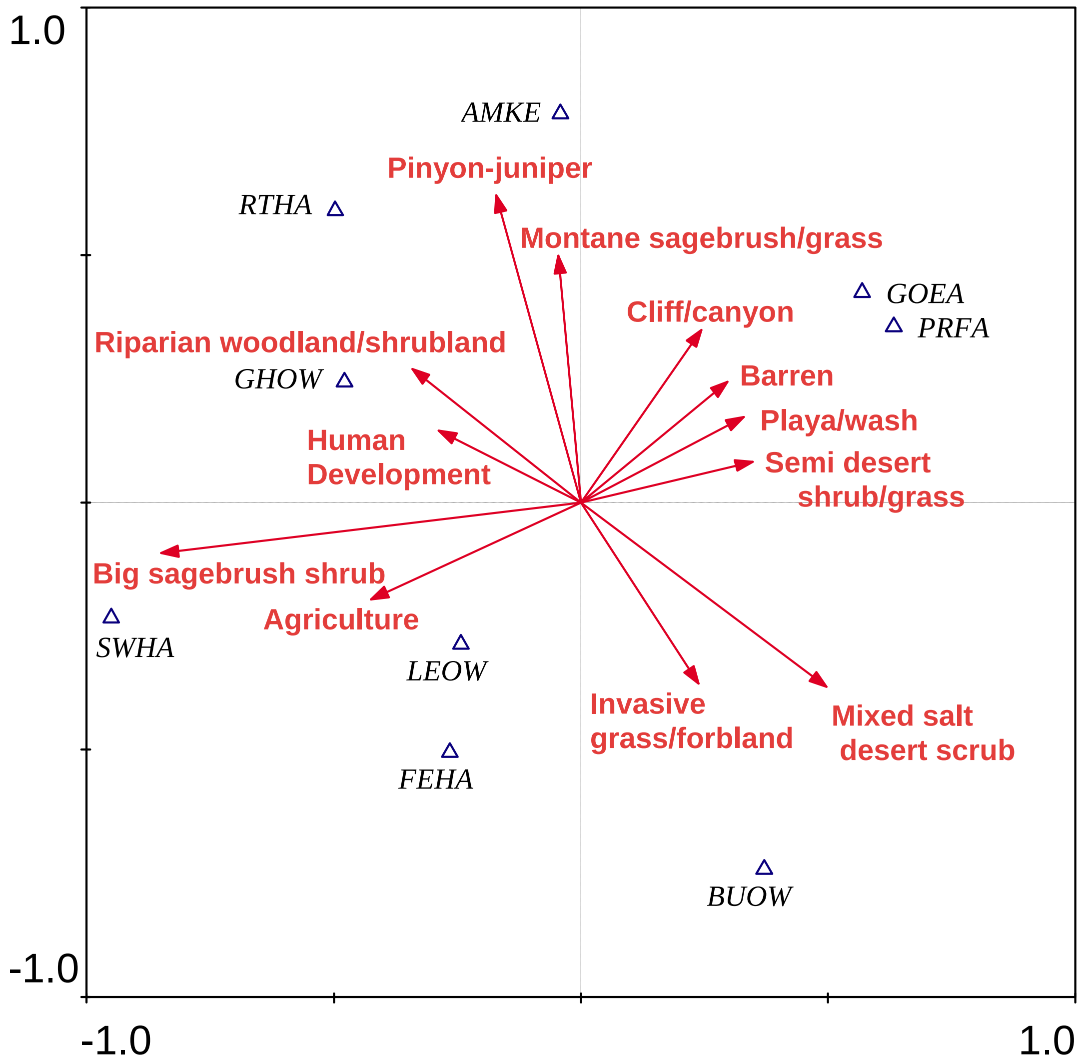

Figure 13. Ordination of raptor species (blue triangles; $n \geq 10$ nesting territories; AMKE = American Kestrel; BUOW = Burrowing Owl; FEHA = Ferruginous Hawk; GHOW = Great Horned Owl; GOEA = Golden Eagle; LEOW = Long-eared Owl; PRFA = Prairie Falcon; RTHA = Red-tailed Hawk; SWHA = Swainson's Hawk) based on vegetation/habitat variables (red arrows) measured within 2 km of nesting territories. Only the first 12 variables accounting for 90% of the variation in the ordination axes are displayed for ease of interpretation.

Modelling Landscape Correlates of Territory Activity

Annual Territory Activity

We identified a single top model to distinguish between active (n = 403) and inactive (n = 289) Golden Eagle territories, which suggested that VF4 and VF5 measured at the average home-range (3.0-km radius) scale were most strongly correlated with annual territory activity (Table 17). Inspection of the variable loadings on these VFs indicated that a positive association with VF4 suggested primarily that the probability of activity increased in areas where coverage of semi-desert shrub/grass and, to lesser degrees, cliff/canyon, marsh, and mixed sagebrush shrub were relatively low, but coverage of greasewood and mixed salt desert scrub were relatively high. A negative association with VF5 further suggested that activity increased in areas where coverage of playa/wash, barren land, cliff/canyon, riparian woodland/shrubland, and agriculture were relatively low. A very low McFadden's ρ^2 value (2.6%) indicated that this model reflected little explanatory power, however. The highest ranking nest-site and climate models fared even less well (i.e., ΔAIC values >2), suggesting only very weakly that active territories tended to average more nests per territory and that the probability of activity increased following wetter years and warmer winters (Table 17).

Table 17. Top logistic regression model (ΔAICc <2.0) describing relationships between Golden Eagle annual territory activity (i.e., nest starts) and landscape variables in northwest Utah. Also shown are the highest ranking (i.e., lowest ΔAICc) nest-site and climate models.

MODEL TYPE	SCALE (RADIUS)	VARIABLES IN MODEL	K	ΔAICc	w_i
Landscape	3.0-km	+VF4, -VF5	3	0.00	0.56
Nest Site	NA	+#Nests	2	12.02	<0.01
Climate	NA	+PYPDSI, -PWTemp	3	14.96	<0.01

Note: K = number of parameters, including constant; w_i = Akaike's weight, indicating probability of model given the data (Burnham and Anderson 2002). See Table 3 for model-type and variable descriptions.

We identified nine top landscape models to distinguish between active (n = 180) and inactive (n = 269) Ferruginous Hawk territories. All top models suggested that landscape variables measured at the study-area scale (1.5-km radius) held the highest explanatory power. All or most top models contained VF5 (9), elevation variability (9), and VF6 (8), with no other variables appearing in a majority of the top models (Table 18). These results suggest that annual activity was higher at territories with more human development, water, and mixed conifer cover, but less elevation variability, marshland, and to a lesser degree big sagebrush/grass within 1.5 km of the territory center. Again, however, a relatively low McFadden's ρ^2 value (6.2%) for the top model suggests only limited, overall explanatory power. Additionally, again none of the nest-site or climate models offered better explanatory power (Table 18).

We identified six top landscape models to distinguish between active (n = 272) and inactive (n = 162) Red-Tailed Hawk territories. All top models contained landscape variables measured at the study area/average home range scale (1.0-km radius) and a majority contained VF6 (6), VF7 (6), VF9 (6), and VF2 (5; Table 19). The VF loadings suggested that annual activity was higher at territories with more montane sagebrush/grass, aspen mix, riparian woodland/shrubland, mixed conifer, disturbed, and human development, but less big sagebrush shrub, big sagebrush/grass, invasive grassland/forbland, barren land, and water. Again, a relatively low McFadden's ρ^2 value (7.6%) for the top model suggests only limited, overall explanatory power, and none of the nest-site or climate models offered better explanatory power (Table 19).

Table 18. Top logistic regression models (ΔAICc <2.0) describing relationships between Ferruginous Hawk annual territory activity (i.e., nest starts) and landscape variables in northwest Utah. Also shown are the highest ranking (i.e., lowest ΔAICc) nest-site and climate models.

MODEL TYPE	SCALE (RADIUS)	VARIABLES IN MODEL	K	ΔAICc	w_i
Landscape	1.5-km	+VF1, +VF5, +VF6, -VF8, -ElevSD	6	0.00	0.12
Landscape	1.5-km	-VF3, +VF5, +VF6, -VF7, -ElevSD	6	0.08	0.11
Landscape	1.5-km	-VF2, -VF3, +VF5, +VF6, -ElevSD	6	0.52	0.09
Landscape	1.5-km	-VF3, +VF5, +VF6, -VF8, -ElevSD	6	0.70	0.08
Landscape	1.5-km	+VF2, +VF5, +VF6, -VF7, -VF8, -ElevSD	7	1.13	0.07
Landscape	1.5-km	+VF5, +VF6, -VF8, -ElevSD	5	1.22	0.06
Landscape	1.5-km	+VF5, +VF6, -VF7, -ElevSD	5	1.32	0.06
Landscape	1.5-km	-VF2, -VF3, +VF5, -ElevSD	5	1.59	0.05
Landscape	1.5-km	+VF1, +VF5, +VF6, -ElevSD	5	1.84	0.05
Nest Site	NA	+NSElev, +NSRugg, -NSPpt	3	17.56	<0.01
Climate	NA	+PWPDSI, -PYTemp	3	23.06	<0.01

Note: K = number of parameters, including constant; w_i = Akaike's weight, indicating probability of model given the data (Burnham and Anderson 2002). See Table 3 for model-type and variable descriptions.

Table 19. Top logistic regression models (ΔAICc <2.0) describing relationships between Red-tailed Hawk annual territory activity (i.e., nest starts) and landscape variables in northwest Utah. Also shown are the highest ranking (i.e., lowest ΔAICc) nest-site and climate models.

MODEL TYPE	SCALE (RADIUS)	VARIABLES IN MODEL	K	ΔAICC	WI
Landscape	1.0-km	+VF2, -VF6, -VF7, +VF8, -VF9	6	0.00	0.15
Landscape	1.0-km	-VF1, +VF2, +VF5, -VF6, -VF7, -VF9	7	0.28	0.13
Landscape	1.0-km	-VF1, +VF2, +VF3, -VF6, -VF7, -VF9	7	0.61	0.11
Landscape	1.0-km	+VF2, +VF3, -VF6, -VF7, -VF9	6	0.82	0.10
Landscape	1.0-km	-VF1, +VF2, -VF6, -VF7, -VF9	6	1.12	0.08
Landscape	1.0-km	+VF3, -VF6, -VF7, -VF9	5	1.33	0.08
Nest Site	NA	+NSPpt, -NSRugg, -#Nests	4	17.98	<0.01
Climate	NA	+PWTemp	2	28.37	<0.01

Note: K = number of parameters, including constant; w_i = Akaike's weight, indicating probability of model given the data (Burnham and Anderson 2002). See Table 3 for model-type and variable descriptions.

We identified a single top nest-site model to distinguish between active (n = 214) and inactive (n = 159) Swainson's Hawk territories, which suggested that annual activity was greater at territories containing more nests and with more mesic nest sites (i.e., higher long-term-average precipitation at nest sites; Table 20). A low McFadden's ρ^2 (3.3%) again suggested limited overall explanatory and no landscape or climate models fared better (Table 19).

Table 20. Top logistic regression model (ΔAICc <2.0) describing relationships between Swainson's Hawk annual territory activity and nest-site variables in northwest Utah. Also shown are the highest ranking (i.e., lowest ΔAICc scores) landscape and climate models.

MODEL TYPE	SCALE (RADIUS)	VARIABLES IN MODEL	K	ΔAICc	w_i
Nest Site	NA	+#Nests, +NSPpt	3	0.00	0.77
Landscape	1.5-km	-VF1	2	5.69	0.05
Climate	NA	+PYTemp	2	9.28	0.01

Note: K = number of parameters, including constant; w_i = Akaike's weight, indicating probability of model given the data (Burnham and Anderson 2002). See Table 3 for model-type and variable descriptions.

We also identified a single top model to distinguish between active (n = 244) and inactive (n = 210) Prairie Falcon territories, suggesting that Prairie Falcon annual activity was higher at territories containing more nests and more mesic and lower-elevation nest sites (Table 21). The McFadden's ρ^2 values of the top nest site (4.8%) model again suggested low overall explanatory power and no landscape models were competitive (Table 21). No significant climate models were created.

Table 21. Top logistic regression models (ΔAICc <2.0) describing relationships between Prairie Falcon annual territory activity and nest-site and landscape variables in northwest Utah. Also shown is the highest ranking (i.e., lowest ΔAICc) landscape model. No significant climate models emerged.

MODEL TYPE	SCALE (RADIUS)	VARIABLES IN MODEL	K	ΔAICc	w_i
Nest Site	NA	+#Nests, +NSPpt, -NSElev	4	0.00	0.48
Landscape	2.0-km	-VF2, +VF3, -VF5, +VF6, -VF7, -VF8, +VF9	8	3.59	0.08

Note: K = number of parameters, including constant; w_i = Akaike's weight, indicating probability of model given the data (Burnham and Anderson 2002). See Table 3 for model-type and variable descriptions.

We identified two top models to distinguish between annually occupied (*n* = 241) and unoccupied (*n* =331) Burrowing Owl burrows. Both top models contained climate variables and suggested that burrow occupancy was greater following years that were warmer and wetter overall but with a relatively cool, dry winter (Table 22). The McFadden's ρ^2 value (2.5%) for the top model was again low, and no landscape or nest-site models provided better explanatory power (Table 22).

Table 22. Top logistic regression models (ΔAICc <2.0) describing relationships between Burrowing Owl annual territory occupancy and climate variables in northwest Utah. Also shown are the highest ranking (i.e., lowest ΔAICc scores) landscape and nest-site models.

MODEL TYPE	SCALE (RADIUS)	VARIABLES IN MODEL	K	ΔAICc	w_i
Climate	NA	+PYTemp, -PWTemp	3	0.00	0.55
Climate	NA	+PYTemp, +PYPDSI, -PWTemp, -PWPDSI	5	1.43	0.27
Landscape	1.0	-VF3	2	10.55	<0.01
Nest Site	NA	-NSRugg, +NSElev	3	12.44	<0.01

Note: K = number of parameters, including constant; w_i = Akaike's weight, indicating probability of model given the data (Burnham and Anderson 2002). See Table 3 for model-type and variable descriptions.

Proportional Territory Activity

We identified a single top proportional-activity model for Golden Eagles (*n* = 96), containing a nest-site variable which suggested that the proportion of years a Golden Eagle territory was active was higher in territories with more nests (Table 23). Models containing landscape variables were less competitive (Table 23). The adjusted r^2 value of the top model (10.2%) suggested that models of Golden Eagle proportional territory activity performed much better than those seeking to explain annual activity (2.6%).

Table 23. Top linear regression models (ΔAICc <2.0) describing the relationship between proportional activity (i.e., proportion of survey years a nest start was recorded) of Golden Eagle territories and a nest-site variable in northwest Utah. Also shown is the highest ranking (i.e., lowest ΔAICc scores) landscape model.

MODEL TYPE	SCALE (RADIUS)	VARIABLES IN MODEL	K	ΔAICc	w_i
Nest Site	NA	+#Nests	2	0.00	0.50
Landscape	3.0-km	-VF1, +VF4, -VF5	4	3.04	0.11

Note: K = number of parameters, including constant; w_i = Akaike's weight, indicating probability of model given the data (Burnham and Anderson 2002). See Table 3 for model-type and variable descriptions.

We identified eight top proportional-activity models for Ferruginous Hawk territories (n = 59), all containing landscape variables (Table 24). All but the lowest ranking of these models suggested that landscape variables measured at the study-area scale (1.5-km radius) provided the highest explanatory power. A negative relationship with elevation variability occurred in six of the top models and with VF2 in six of the seven top 1.5-km-scale models. Similarly, a positive relationship with VF5 was indicated in four of the top 1.5-km-scale models. A consistent negative association with VF2 suggested primarily higher activity at territories with relatively high cover of invasive grass/forbland and semi-desert shrub/grass, with lesser negative associations related to mixed salt desert scrub, mixed sagebrush shrub, greasewood, and barren land. A consistent positive association with VF5 suggested primarily higher activity at territories with more human development and, to a lesser degree, more water. The final 2.0-km-scale top model included VF2, VF3, VF6 and elevation variability, suggesting higher activity at territories with a greater cover of invasive grass/forblands and semi-desert shrub/grass, consistent with the 1.5-km-scale relationships, but also more mixed conifer and big sagebrush shrub and less cliff/canyon and elevation variability within 2.0 km. The adjusted r^2 values for the top model was 21.6%. Models containing nest-site variables were not competitive with the top landscape models (Table 24).

Table 24. Top linear regression models (ΔAICc <2.0) describing relationships between proportional activity (i.e., proportion of survey years a nest start was recorded) of Ferruginous Hawk territories and landscape variables in northwest Utah. Also shown is the highest ranking (i.e., lowest ΔAICc scores) nest-site model.

MODEL TYPE	SCALE (RADIUS)	VARIABLES IN MODEL	K	ΔAICc	w_i
Landscape	1.5-km	-VF2, -VF3, +VF5, -ElevSD	5	0.00	0.09
Landscape	1.5-km	+VF6, -ElevSD	3	0.04	0.09
Landscape	1.5-km	-VF2, +VF5, +VF6, -ElevSD	5	0.30	0.08
Landscape	1.5-km	+VF1, -VF2, +VF5, +VF7, -ElevSD	6	1.01	0.05
Landscape	1.5-km	-VF2, -VF3, +VF5	4	1.19	0.05
Landscape	1.5-km	-VF2, -ElevSD	3	1.60	0.04
Landscape	1.5-km	+VF1, -VF2, +VF7	5	1.74	0.04
Landscape	2.0-km	-VF2, -VF3, +VF6, -ElevSD	5	1.92	0.03
Nest Site	NA	+NSElev	2	7.02	<0.01

Note: K = number of parameters, including constant; w_i = Akaike's weight, indicating probability of model given the data (Burnham and Anderson 2002). See Table 3 for model-type and variable descriptions.

We identified four top proportional-activity models for Red-tailed Hawk territories (n = 47), all including landscape variables (Table 25). The first, third, and fourth top models included landscape variables measured at the study-area/average-home-range scale (1.0-km radius), whereas the second top model contained variables measured at the upper-home-range scale (2.0-km radius). The three 1.0-km models all included a positive association with VF3, suggesting higher activity at territories with relatively high cover of agriculture and human development and low cover of mixed sagebrush shrub and, to a lesser degree, semi-desert shrub/grass. Two of the three models also included a positive association with VF4, suggesting higher activity at territories with less invasive grass/forbland and semi-desert shrub/grass, and, to a lesser degree, more big sagebrush shrub. The 2.0-km-scale model included associations with three VFs, which collectively painted a complex picture, but reflected at least some consistencies with the 1.0-km models. These included positive associations with agriculture and human development, and negative associations with mixed sagebrush shrub and semi-desert shrub/grass. Other relatively high-scoring relationships in the 2.0-km model included a positive association with playa/wash but negative association with barren land. The top 1.0 and 2.0-km scale models performed reasonably well, with adjusted r^2 values of 34.6% and 36.1%, respectively. Models with nest-site variables were not competitive (Table 25).

Table 25. Top linear regression models (ΔAICc <2.0) describing relationships between proportional activity (i.e., proportion of survey years a nest start was recorded) of Red-tailed Hawk territories and landscape variables in northwest Utah. Also shown is the highest ranking (i.e., lowest ΔAICc scores) nest-site model.

MODEL TYPE	SCALE (RADIUS)	VARIABLES IN MODEL	K	ΔAICc	w_i
Landscape	1.0-km	+VF3, -VF7	3	0.00	0.17
Landscape	2.0-km	+VF3, +VF4, -VF7	4	0.25	0.15
Landscape	1.0-km	+VF3, +VF4, -VF5	4	0.40	0.14
Landscape	1.0-km	+VF3, +VF4, -VF8	4	1.85	0.07
Nest Site	NA	-NSRugg, +NSPpt	3	11.85	<0.01

Note: K = number of parameters, including constant; w_i = Akaike's weight, indicating probability of model given the data (Burnham and Anderson 2002). See Table 3 for model-type and variable descriptions.

We identified two top proportional-activity models for Swainson's Hawk territories (n = 49). Both contained nest-site variables and suggested that proportional activity was greater at territories with more nests (Table 26). Otherwise, both models contained different second variables, with the top model suggesting that activity was greater at higher-elevation territories and the second model suggesting that activity was greater at more mesic sites. The r^2 value for the top model was a respectable 25.5%. Models with landscape variables were not competitive (Table 26).

Table 26. Top linear regression models (ΔAICc <2.0) describing relationships between proportional activity (i.e., proportion of survey years a nest start was recorded) of Swainson's Hawk territories and nest-site variables in northwest Utah. Also shown is the highest ranking (i.e., lowest ΔAICc scores) landscape model.

MODEL TYPE	SCALE (RADIUS)	VARIABLES IN MODEL	K	ΔAICc	w_i
Nest Site	NA	+#Nests, +NSElev	3	0.00	0.50
Nest Site	NA	+#Nests, +NSPpt	3	0.52	0.38
Landscape	5.0-km	+ElevSD	2	8.70	0.01

Note: K = number of parameters, including constant; w_i = Akaike's weight, indicating probability of model given the data (Burnham and Anderson 2002). See Table 3 for model-type and variable descriptions.

We identified a single top proportional activity model for Prairie Falcon territories (*n* = 48). The top model contained nest-site variables and suggested that proportional activity was higher at territories with more nests and less terrain ruggedness (Table 27). The adjusted r^2 value of the top model was again a respectable 31.8%. Models with landscape variables were not competitive (Table 27).

Table 27. Top linear regression models (ΔAICc <2.0) describing relationships between proportional activity (i.e., nest starts per survey years) of Prairie Falcon territories and nest site variables in northwest Utah. Also shown is the highest ranking (i.e., lowest ΔAICc scores) landscape model.

MODEL TYPE	SCALE (RADIUS)	VARIABLES IN MODEL	K	ΔAICc	w_i
Nest Site	NA	+#Nests, -NSRugg	3	0.00	0.69
Landscape	2.0-km	+VF2, -VF7, -ElevSD	4	3.84	0.10

Note: K = number of parameters, including constant; w_i = Akaike's weight, indicating probability of model given the data (Burnham and Anderson 2002). See Table 3 for model-type and variable descriptions.

We identified four top models to describe relationships concerning proportional occupancy of Burrowing Owl burrows (*n* = 68). The top model contained nest-site variables and suggested that proportional occupancy increased at higher elevations and in areas of relatively low terrain ruggedness (Table 28). The remaining three top models were landscape models measured at the upper-home-range scale. The top upper-home-range-scale model contained VF2, which suggested that occupancy rates tended to increase in areas where coverage of big sagebrush shrub, mixed sagebrush, pinyon-juniper, and, to lesser degrees, montane sagebrush/grass, montane shrub/scrub, and aspen mix were relatively high and coverage of greasewood, invasive grass/forbland, marsh, and playa/wash were relatively low within 1.5 km of the burrow. In contrast, the other model from this scale contained VF3 and VF10, which suggested occupancy was higher where there was more big sagebrush shrub, big sagebrush/grass, agriculture, and water, but less mixed salt desert scrub and cliff/canyon cover within 1.5 km of the burrow. The top home-range-scale model contained VF3 and VF5 and suggested that occupancy rates were higher in areas where coverage of water, big sagebrush shrub, and mixed sagebrush was higher, but cover of semi-desert shrub/grass, montane shrub/scrub, invasive grass/forbland, and conifer was lower within 1.0 km of the burrow. All of the top landscape models suggested proportional occupancy was positively related to big sagebrush cover, but negatively related to invasive grass/forbland. The adjusted r^2 values of the top nest-site model (11.1%), 1.5-km landscape model (7.8%), and 1.0-km landscape model (8.5%) all reflected better performance than the top annual-occupancy model for the species (2.5%).

Table 28. Top linear regression models (ΔAICc <2.0) describing relationships between proportional occupancy (i.e., proportion of survey years that a burrow was occupied) of Burrowing Owl burrows and nest-site and landscape variables in northwest Utah.

MODEL TYPE	SCALE (RADIUS)	VARIABLES IN MODEL	K	ΔAICc	w_i
Nest Site	NA	+NSElev, -NSRugg	3	0.00	0.20
Landscape	1.5-km	-VF2	2	1.34	0.10
Landscape	1.5-km	+VF3, +VF10	3	1.60	0.09
Landscape	1.0-km	-VF3, +VF5	3	1.98	0.07

Note: K = number of parameters, including constant; w_i = Akaike's weight, indicating probability of model given the data (Burnham and Anderson 2002). See Table 3 for model-type and variable descriptions.

Nest Survival

We identified a single top model to describe relationships between climate variables and the probability of a Golden Eagle nest surviving (*n* = 337 observation intervals) or failing (*n* = 71). This model suggested that the likelihood of nest survival increased following cooler years and when the nesting season was relatively wet (Table 29). The McFadden's ρ^2 value of this model was 9.3%, indicating moderate, overall explanatory power. Models containing landscape variables were not competitive and no significant nest-site models emerged.

Table 29. Top logistic exposure model (ΔAICc <2.0) describing the relationship between Golden Eagle nest survival and climate variables in the northwest Utah study area. The highest ranking (i.e., lowest ΔAICc scores) landscape model is also displayed in italics. No significant nest site models were created.

MODEL TYPE	SCALE (RADIUS)	VARIABLES IN MODEL	K	ΔAICc	w_i
Climate	NA	-PYTemp, +NSPDSI	3	0.00	0.59
Landscape	5.0-km	-VF6	2	27.06	<0.01

Note: K = number of parameters, including constant; w_i = Akaike's weight, indicating probability of model given the data (Burnham and Anderson 2002). See Table 3 for model-type and variable descriptions.

We identified three top nest-survival models for Ferruginous Hawks (*n* = 155 successful observation intervals and 17 failures). All top models were composed of landscape variables measured at the study-area scale (1.5-km radius; Table 30). All three models contained VF2, VF5, VF6, and VF8. A positive association with VF2 primarily suggested that the likelihood of nest survival increased in areas where coverage of invasive grass/forbland and semi-desert shrub/grass were relatively low. A positive association with VF5 primarily suggested that the likelihood of nest survival increased in areas of relatively high human development and, to a lesser degree, water coverage. A negative association with VF6 primarily suggested that the likelihood of nest survival increased in areas of relatively low mixed conifer cover and, to a lesser degree, high marsh cover; however, the relationship with marsh cover appeared mixed as the VF2 factor also included a moderate negative association with marsh. One model also suggested nest survival increased where elevation variability was lower within 1.5 km. The top study-area scale model achieved a moderate McFadden's ρ^2 value of 14.9%. The highest-ranking climate and nest-models were less competitive, but only marginally so, and the best of these indicated a weak positive relationship with previous-year moisture levels and a weak negative relationship with nest height (Table 30).

Table 30. Top logistic exposure models (ΔAICc <2.0) describing relationships between Ferruginous Hawk nest survival and landscape variables in northwest Utah. Also shown are the highest ranking (i.e., lowest ΔAICc scores) climate and nest-site models.

MODEL TYPE	SCALE (RADIUS)	VARIABLES IN MODEL	K	ΔAICc	w_i
Landscape	1.5-km	+VF2, -VF4, +VF5, +VF6, -VF8	6	0.00	0.26
Landscape	1.5-km	+VF2, +VF5, +VF6, -VF8	5	0.48	0.21
Landscape	1.5-km	+VF2, +VF3, +VF5, +VF6, -VF7, -VF8, -ElevSD	8	1.67	0.11
Climate	NA	+PYPDSI	2	3.67	0.08
Nest Site	NA	-NSHgt	2	5.72	0.02

Note: K = number of parameters, including constant; w_i = Akaike's weight, indicating probability of model given the data (Burnham and Anderson 2002). See Table 3 for model-type and variable descriptions.

We identified five top nest-survival models for Red-tailed Hawks (*n* = 338 successful observation intervals and 26 failures). All contained landscape variables, with the top three and fifth-ranked models containing variables measured at the upper-home-range scale (2.0-km radius) and the fourth-ranked model containing variables measured at the study-area/average-home-range scale (1.0-km radius; Table 31). Three of the four 2.0-km models included VF8 and two included VF2. A positive association with VF8 suggested that nest survival increased in areas with relatively high cover of montane shrub/scrub, pinyon-juniper, cliff/canyon, and water, and relatively low cover of mixed conifer and big sagebrush/grass. A negative association with VF2 suggested that nest survival increased in areas with relatively low cover of aspen mix, montane sagebrush/grass, and mixed conifer, and relatively high cover of big sagebrush shrub and agriculture. Thus, the two factors reflected mixed patterns relative mixed conifer and big sagebrush habitats, depending on what other habitat types were involved. The 1.0-km model included only VF2, with a negative association suggesting that nest survival increased in areas with relatively low cover of aspen mix, montane sagebrush/grass, and, to lesser degrees, mixed conifer, cliff/canyon, and montane sagebrush shrub, but relatively high cover of big sagebrush shrub. McFadden's ρ^2 values of 4.9% and 3.2% for the top 2.0-km and 1.0-km models, respectively, did not perform well in explaining variability in Red-tailed Hawk nest survival. The highest-ranking nest-site model performed less well but only barely fell outside of the ΔAICc cutoff of 2.0; it suggested that nest survival increased at lower elevations (Table 31). No significant climate models emerged.

Table 31. Top logistic exposure models (ΔAICc <2.0) describing relationships between Red-tailed Hawk nest survival and landscape variables in northwest Utah. Also shown is the highest ranking (i.e., lowest ΔAICc scores) nest-site model. No significant climate models emerged.

MODEL TYPE	SCALE (RADIUS)	VARIABLES IN MODEL	K	ΔAICc	w_i
Landscape	2.0-km	-VF2, +VF8	3	0.00	0.19
Landscape	2.0-km	-VF6, +VF8	3	0.15	0.18
Landscape	2.0-km	-VF2	2	0.53	0.14
Landscape	1.0-km	-VF2	2	1.07	0.11
Landscape	2.0-km	-VF1, -VF7, +VF8	4	1.61	0.08
Nest Site	NA	-NSElev	2	2.25	0.06

Note: K = number of parameters, including constant; w_i = Akaike's weight, indicating probability of model given the data (Burnham and Anderson 2002). See Table 3 for model-type and variable descriptions.

We identified a single top nest-survival model for Swainson's Hawks (*n* = 225 successful observation intervals and 29 failures) which contained a single climate variable and suggested that the probability of nest survival increased following warmer years (Table 32). The McFadden's ρ^2 value of the model (7.2%) suggested only fair predictive ability. Models containing nest-site or landscape variables were not competitive with the top climate model (Table 32), but weakly suggested higher survival in higher nests, at less rugged sites, and in habitats with relatively high cover of agriculture, semi-desert shrub/grass, and water, but lower cover of playa/wash, marsh, and big sagebrush/grass.

Table 32. Top logistic exposure model (ΔAICc <2.0) describing relationships between Swainson's Hawk nest survival and climate variables in northwest Utah. Also shown are the highest ranking (i.e., lowest ΔAICc scores) nest-site and landscape models.

MODEL TYPE	SCALE (RADIUS)	VARIABLES IN MODEL	K	ΔAICc	w_i
Climate	NA	+PYTemp	2	0.00	0.70
Nest Site	NA	-NSRugg, +NSHgt	3	6.29	0.03
Landscape	1.5-km	-VF6	2	7.67	0.02

Note: K = number of parameters, including constant; w_i = Akaike's weight, indicating probability of model given the data (Burnham and Anderson 2002). See Table 3 for model-type and variable descriptions.

We identified three top nest-survival models for Prairie Falcons (*n* = 156 successful observation intervals and 28 failures) represented by landscape models (Table 33). The two top models included landscape variables measured at the upper-home-range scale (10.0-km radius). Both contained VF3 and elevation variability, and suggested that nest survival increased in areas with lower elevational diversity, relatively high cover of playa/wash, cliff/canyon, semi-desert shrub/grass, exposed rock, and barren land, and relatively low cover of mixed salt desert scrub, mixed sagebrush shrub, and big sagebrush shrub within 10.0-km radii of nests. The third top model included four landscape variables (VFs) measured at the average-home-range scale (5.0-km radius). The combination of variables suggested that nest survival increased in areas with relatively high cover of invasive grass/forbland, greasewood, human development, marsh, and water, but less mixed sagebrush shrub, mixed salt desert scrub, exposed rock, cliff/canyon, disturbed, and barren land within a 5.0-km radius of the nest. McFadden's ρ^2 values suggested similar, moderate performance for the top upper-home-range (13.0%) and average-home-range (12.6%) models. In comparison, the highest-ranking climate and nest-site models, though significant, were not competitive (Table 33).

Table 33. Top logistic exposure models (ΔAICc <2.0) describing relationships between Prairie Falcon nest survival and landscape and nest site variables in northwest Utah. Also shown is the highest ranking (i.e., lowest ΔAICc scores) climate model.

MODEL TYPE	SCALE (RADIUS)	VARIABLES IN MODEL	K	ΔAICc	w_i
Landscape	10.0-km	-VF1, +VF3, +VF6, -ElevSD	5	0.00	0.22
Landscape	5.0-km	-VF2, +VF4, -VF6, +VF7	5	0.61	0.15
Landscape	10.0-km	+VF3, -VF4, +VF5, -ElevSD	5	0.69	0.14
Climate	NA	-PYTemp, +NSPDSI	3	10.49	<0.01
Nest Site	NA	+NSPpt	2	10.68	<0.01

Note: K = number of parameters, including constant; w_i = Akaike's weight, indicating probability of model given the data (Burnham and Anderson 2002). See Table 3 for model-type and variable descriptions.

Nest Productivity

We identified six top productivity models for Golden Eagles (*n* = 217 relevant nest starts). All six models involved landscape variables, with the top-ranked model represented by variables measured at the study-area scale (0.5-km radius) and the remaining five models represented by variables measured at the average-home-range scale (3.0-km radius; Table 34). The top 0.5-km model included positive associations with VF4 and VF5. Inclusion of VF4 suggested that the productivity of successful nests increased in areas with relatively low cover of semi-desert shrub/grass and invasive grass/forbland, and, to lesser degrees, less cliff/canyon and more greasewood within a 0.5-km radius of the nest. Inclusion of VF5 suggested higher productivity in areas with relatively high cover of barren land, cliff/canyon, and playa/wash. Thus, the two variables presented conflicting indicators relative to cliff/canyon habitats. The five 3.0-km models all included VF5; no other variables appeared in a majority of the five models, but VF2, VF4, and VF7 all appeared in two models each (although in both cases the *P*-values for VF4 were >0.05). A positive association with VF5 suggested that productivity increased in areas with relatively high cover of playa/wash, barren land, cliff/canyon, and, to lesser degrees, high cover of riparian woodland/shrubland and agriculture, but low cover of invasive grass/forbland within a 3.0-km radius of the nest. A negative association with VF2 suggested higher productivity in areas of relatively high cover of big sagebrush shrub, pinyon-juniper, and agriculture, but low cover of aspen mix and mixed conifer. A negative association with VF7 suggested higher productivity in disturbed areas and where marsh and water were relatively scarce. The adjusted r^2 values of the top 1.0-km and 3.0-km models were 4.6% and 4.5%, respectively, indicating overall poor explanatory power. The highest-ranking nest-site model was not competitive (Table 34) and no significant climate models emerged.

Table 34. Top linear regression models (ΔAICc <2.0) describing relationships between the productivity of successful Golden Eagle nests and landscape variables in northwest Utah. Also shown is the highest ranking (i.e., lowest ΔAICc scores) nest-site model. No significant climate models emerged.

MODEL TYPE	SCALE (RADIUS)	VARIABLES IN MODEL	K	ΔAICc	w_i
Landscape	0.5-km	+VF4, +VF5	3	0.00	0.14
Landscape	3.0-km	-VF1, +VF5	3	0.32	0.12
Landscape	3.0-km	-VF2, +VF5	3	0.70	0.10
Landscape	3.0-km	-VF2, +VF4, +VF5, +ElevSD	5	0.81	0.09
Landscape	3.0-km	+VF4, +VF5, -VF7	4	1.30	0.07
Landscape	3.0-km	+VF5, -VF7	3	1.39	0.07
Nest Site	NA	-#Nests	2	7.22	<0.01

Note: K = number of parameters, including constant; w_i = Akaike's weight, indicating probability of model given the data (Burnham and Anderson 2002). See Table 3 for model-type and variable descriptions.

We identified four top productivity models for Ferruginous Hawks (*n* = 112 relevant nest starts). The first- and third-ranked models included climate variables and the other two included landscape variables measured at the upper-home-range scale (5.0-km radius; Table 35). In combination, the two climate models suggested that the productivity of successful nests increased following warmer years but when the current nesting season was cooler. The top-ranked landscape model contained a single variable (VF4) and suggested that productivity was greater in areas with less human development and disturbed land, and, to lesser degrees, less agriculture but more mixed conifer and mixed sagebrush shrub within a 5.0-km radius of the nest. The second top landscape model contained VF2 and VF7. A positive association with VF2 suggested primarily that productivity increased in areas with more semi-desert shrub/grass, invasive grass/forbland, and disturbed habitat, and less mixed and big sagebrush shrub within a 5.0-km radius of the nest. A negative association with VF7 suggested that productivity increased in areas with more mixed sagebrush shrub, pinyon-juniper, and disturbed land, but less mixed conifer and greasewood. Thus, the two variables in this model as well as the two landscape models reflected conflicting indicators relative to mixed sagebrush shrub habitats, and the two landscape models also reflected conflicting indicators relative to the influences of disturbed land. We conclude that the combination of indicators suggests an overall negative influence of disturbed land and positive influence of mixed sagebrush shrub, but that there clearly are habitat combinations whereby the opposite is true for both habitat types. Adjusted r^2 values of 4.5% for the top climate model and 4.2% for the top landscape model again suggested relatively poor explanatory power. No significant nest-site models emerged.

Table 35. Top regression models (ΔAICc <2.0) describing relationships between the productivity of successful Ferruginous Hawk nests and climate and landscape variables in northwest Utah. No significant nest-site models emerged.

MODEL TYPE	SCALE (RADIUS)	VARIABLES IN MODEL	K	ΔAICc	w_i
Climate	NA	-NSTemp	2	0.00	0.15
Landscape	5.0-km	+VF4	2	0.40	0.13
Climate	NA	+PYTemp	2	0.81	0.10
Landscape	5.0-km	+VF2, -VF7	3	1.00	0.09

Note: K = number of parameters, including constant; w_i = Akaike's weight, indicating probability of model given the data (Burnham and Anderson 2002). See Table 3 for model-type and variable descriptions.

We identified two top productivity models for Red-tailed Hawks (*n* = 183 relevant nest starts). Both included landscape variables measured at the study-area/average-home-range scale (1.0-km radius) and both included negative associations with VF6 and VF9, while the top model also included a negative association with VF3 (Table 36). The combination consistently suggested that productivity increased in areas with relatively high cover of mixed sagebrush/grass and low cover of big sagebrush/grass, marsh, and water within a 1.0-km radius of the nest. Other habitat variables associated with relatively high loadings but for which the combination of variables suggested mixed relationships included agriculture (a mostly negative relationship), disturbed land (a mostly positive relationship), greasewood, human development, invasive grass/forbland (notably highest loading a negative relationship), montane shrub/scrub (notably highest loading a negative relationship), pinyon-juniper, playa/wash (a mostly negative relationship), riparian woodland/shrubland, and semi-desert shrub/grass. The adjusted r^2 value for the top model was 5.1%, indicating poor overall explanatory power. The highest-ranking climate model fared less well, but weakly suggested higher productivity following warmer years and at drier sites (Table 36). No significant nest-site models emerged.

Table 36. Top regression models (ΔAICc <2.0) describing relationships between the productivity of successful Red-tailed Hawk nests and landscape variables in northwest Utah. Also shown is the highest ranking (i.e., lowest ΔAICc scores) climate model. No significant nest-site models emerged.

MODEL TYPE	SCALE (RADIUS)	VARIABLES IN MODEL	K	ΔAICc	w_i
Landscape	1.0-km	-VF3, -VF6, -VF9	4	0.00	0.27
Landscape	1.0-km	-VF6, -VF9	3	0.55	0.21
Climate	NA	+PYTemp, -NSPDSI	3	4.33	0.03

Note: K = number of parameters, including constant; w_i = Akaike's weight, indicating probability of model given the data (Burnham and Anderson 2002). See Table 3 for model-type and variable descriptions.

We identified four top productivity models for Swainson's Hawks (*n* = 108 relevant nest starts). The first three top models contained landscape variables measured at the average-home-range scale (3.0-km radius) and all three included VF1, VF2, and VF7. The top model also included a negative association with elevation variability. The combination of habitat variables consistently suggested that productivity increased in areas with relatively low cover of invasive grass/forbland and marsh within a 3.0-km radius of the nest. Indicators for all other original habitat variables were mixed, but notably stronger or mostly positive associations were indicated for big and mixed sagebrush shrub, pinyon-juniper, and water, whereas notably stronger or mostly negative associations were indicated for greasewood, mixed salt desert scrub, and playa/wash.. The fourth top model included VF1, VF5, and VF7 measured at the upper-home-range scale (5.0-km radius). The combination of variables consistently suggested positive associations with agriculture, aspen mix, mixed conifer, montane sagebrush/grass, and water. Indicators for all other original habitat variables were mixed, but notably stronger or mostly positive associations were indicated for big sagebrush shrub, whereas notably stronger or mostly negative associations were indicated for barren land, cliff/canyon, marsh, mixed sagebrush shrub, mixed salt desert scrub, playa/wash, and semi-desert shrub/grass. The adjusted r^2 value of the top average-home-range (9.0%) and upper-home-range models (6.9%) indicated fair explanatory power. The highest ranking climate and nest-site models fared less well, but weakly suggested that productivity tended to increase following warmer and wetter years and during warmer nesting seasons, and tended to be higher in territories with more nests (Table 37).

Table 37. Top regression models (ΔAICc <2.0) describing relationships between the productivity of successful Swainson's Hawk nests and landscape variables in northwest Utah. Also shown are the highest ranking (i.e., lowest ΔAICc scores) climate and nest-site models.

MODEL TYPE	SCALE (RADIUS)	VARIABLES IN MODEL	K	ΔAICc	w_i
Landscape	3.0-km	+VF1, -VF2, +VF7, -ElevSD	5	0.00	0.13
Landscape	3.0-km	+VF1, -VF2, -VF3, +VF7	5	0.03	0.13
Landscape	3.0-km	+VF1, -VF2, +VF7	4	0.97	0.08
Landscape	5.0-km	+VF1, +VF5, -VF7	4	1.31	0.07
Climate	NA	+PYPDSI, +PYTemp, +NSTemp	4	3.29	0.03
Nest Site	NA	+#Nests	2	4.92	0.01

Note: K = number of parameters, including constant; w_i = Akaike's weight, indicating probability of model given the data (Burnham and Anderson 2002). See Table 3 for model-type and variable descriptions.

We identified nine top productivity models for Prairie Falcons (n = 135 relevant nest starts). The first four models included landscape variables measured at the study-area scale (2.0-km radius); the sixth included nest-site variables, and the remaining four included landscape variables measured at the average-home-range scale (5.0-km radius; Table 38). The top landscape model uniquely included VF1, as well as VF9, which appeared in one other of the 2.0-km landscape models. A positive association with VF1 suggested higher productivity in areas with relatively high cover of riparian woodland/shrubland, big sagebrush/grass, big sagebrush shrub, pinyon-juniper, agriculture, and/or montane sagebrush/grass, and relatively low cover of mixed salt desert scrub within a 2.0-km radius of the nest. A negative association with VF9 suggested higher productivity in areas where cover of mixed conifer was relatively low. All other 2.0-km models contained VF3 and VF4. A negative association with VF3 suggested higher productivity in areas with relatively high cover of cliff/canyon, montane sagebrush/grass, aspen mix, and, to lesser degrees, barren land and playa/wash, and relatively low cover of big and mixed sagebrush shrub. A positive association with VF4 suggested higher productivity in areas with relatively high cover of mixed sagebrush shrub and relatively low cover of greasewood and human development. Thus, the two-variable combination reflected mixed influences of mixed sagebrush shrub, and the top model and the following three 2.0-km models reflected mixed influences of big sagebrush shrub. Three of four 5.0-km models contained VF3, and VF4 and VF7 each were represented in two models (VF5 also, but with *P* >0.05 in one case). The combination suggested higher productivity in areas with relatively high cover of cliff/canyon, marsh, playa/wash, and/or semi-desert shrub/grass, and relatively low cover of agriculture, big sagebrush shrub, disturbed land, greasewood, and human development within a 5.0-km radius of the nest. Thus, in relation to indicators from the 2.0-km models, the 5.0-km model results reflected mixed messages concerning the influence of agriculture, and further emphasized a negative association with big sagebrush shrub. Finally, the top nest-site model suggested higher productivity at territories with fewer nests and at higher elevations. The adjusted r^2 of the top study-area-scale (6.1%), average-home-range-scale (6.3%), and nest-site (5.2%) models suggested at best fair explanatory power. The highest-ranking climate model was not competitive, but weakly indicated higher productivity during cooler nesting seasons (Table 38).

Table 38. Top regression models (ΔAICc <2.0) describing relationships between the productivity of successful Prairie Falcon nests and landscape and nest-site variables in northwest Utah. Also shown is the highest ranking (i.e., lowest ΔAICc scores) climate model.

Model Type	Scale (radius)	Variables in Model	K	ΔAICc	w_i
Landscape	2.0-km	+VF1, -VF9	3	0.00	0.09
Landscape	2.0-km	-VF3, +VF4, -VF9	4	0.30	0.08
Landscape	2.0-km	-VF3, +VF4, -VF8	4	0.33	0.08
Landscape	2.0-km	-VF3, +VF4	3	0.90	0.06
Landscape	5.0-km	+VF3, -VF5, +VF7	4	0.93	0.06
Nest Site	NA	-#Nests, +NSElev	3	1.28	0.05
Landscape	5.0-km	-VF1, -VF4	3	1.72	0.04
Landscape	5.0-km	+VF3, +VF6, +VF7	4	1.79	0.04
Landscape	5.0-km	+VF3, -VF4, -VF5	4	1.83	0.04
Climate	NA	-NSTemp	2	5.16	<0.01

Note: K = number of parameters, including constant; w_i = Akaike's weight, indicating probability of model given the data (Burnham and Anderson 2002). See Table 3 for model-type and variable descriptions.

DISCUSSION

Study Area Characteristics

The northwest Utah study area is dominated (70%) by a mixture of desert shrub, sagebrush, and grass vegetation. Pinyon-juniper is the most important woodland vegetation within the defined study area (e.g., excluding high-elevation areas) and, not surprisingly, junipers provide the most common tree substrate for nesting raptors in the study area. On the surface, the study area appears largely undisturbed by human influences, with invasive grass/forbland, agriculture, human development, and recently disturbed areas accounting for <11% of the study-area landscape. While it is true that the relatively remote study area has largely escaped significant human settlement, mining, energy development, etc., the influences of more transient disturbances, such as livestock grazing and recreation were not captured by the map layers we used to describe the study area. Our surveyors regularly observed evidence of sheep and cattle grazing, all-terrain vehicle use, and various shooting activities throughout much of the study area and the history of the project.

The vegetation map we did use to describe our study area and investigate the potential influence of vegetation on various parameters of raptor nesting was created by the USGS National Gap Analysis Program (2005). This map was created from imagery collected from 2000–2003 and did not account for potential vegetation changes during later years of the study. Considering the scale of the vegetation map (i.e., 30-m pixels) and the limited number of vegetation divisions it contained, it is unlikely that many relevant, large-scale changes in vegetation occurred during this study. The likely exception to this generalization is fire-related vegetation replacement. Although the vegetation map we used for our analyses suggested that invasive grass/forbland vegetation (primarily cheatgrass) covered only 6.4% of the study area, large fires in the last two years of the study likely increased coverage of this vegetation type, as wholesale conversions to cheatgrass are known to occur as quickly as within 1–3 years following fire (Zouhar 2003).

Drought conditions dominated the 1998–2007 study period and peaked in 2003. Only two relatively wet and cooler years were recorded during the study, occurring in 1998 and 2005 (Figure 5). Not surprisingly, fire was more common and widespread in both two-year periods immediately following these wet years when vegetative biomass (i.e., fuel loads) increased substantially. In contrast, fire occurrence and the area affected by fire were lowest in the midst of the worst drought years (i.e., 2002–2004). Although we did have access to a map layer characterizing the general boundary of fires within the study area (but not their specific characteristics or internal patch configurations), the fact that the most significant fires occurred at the very beginning and end of the study period precluded a rigorous assessment of raptor nesting ecology both pre- and post-fire. Although we documented at least 92 raptor nests within fire boundaries, nests were only rarely destroyed by fire due to their low vulnerability on cliffs, outcrops, or in scattered junipers that did not themselves burn.

NEST-SITE AND TERRITORY DYNAMICS

Distribution of Territories by Landowner

In general, nesting raptors showed little or no preference for public or private lands, as nests were located on both in proportions equal to their distribution in the study area (64% and 35%, respectively). Only the distribution of Red-tailed and Swainson's Hawk nests appeared to be skewed in favor of private lands. These two species regularly nested near agricultural lands associated with private property and in cottonwoods or other planted, deciduous trees located at the edges of fields or near homes. Swainson's Hawks are known to favor agricultural areas for nesting and foraging, provided the planted crops are not too dense or tall (England et al. 1997). The Red-tailed Hawk is an abundant, widespread raptor that uses a wide variety of habitats (Preston and Beane 1993), but also tends to prefer taller nesting substrates than Swainson's and especially Ferruginous Hawks (Janes 1985, Preston and Beane 1993). In this landscape, taller trees located near suitable foraging habitat generally are common only where humans have planted them as windbreaks or around their houses and other activity centers. Red-tailed Hawks also are known to be relatively tolerant of nesting near human habitations; their productivity has even been positively associated with urban density and roads in some areas (Stout et al. 2006).

Nesting Substrates

Golden Eagles and Prairie Falcons in the study area nested almost entirely on cliff and outcrop substrates. This typical for Prairie Falcons (Steenhof 1998), whereas Golden Eagles routinely nest in trees in other regions of their range (Kochert et al. 2002). In this case, however, the regular availability of cliff and outcrop features and a relative lack of suitable large trees largely precluded Golden Eagle use of trees in this study area. In contrast, Ferruginous and Swainson's Hawks nested predominantly in juniper trees, although when not confounded by the presence of nesting Red-tailed Hawks, Swainson's Hawks also took advantage of a variety of other tree species, mostly around human habitations and agricultural landscapes. In this study area, only a handful of Ferruginous Hawk nests have been built directly on the ground, and all were built before and were not used during the study. More known nests of this species were built on very small rock outcrops that are essentially just as accessible as true ground nests, but again only a handful of these nests were used during the study. Although Ferruginous Hawks more commonly nest on the ground and in shrubs elsewhere (Bechard and Schmutz 1995), other studies have shown that they commonly abandon such sites when more secure, elevated substrates are readily available (e.g., Neal et al. in press). In contrast to Ferruginous and Swainson's Hawks, Red-tailed Hawks are known to be habitat generalists (Preston and Beane 1993) and, consistent with this notion, in our study area we found them nesting on a comparatively much broader range of substrates.

Use of Alternate Nest Sites

We documented both single- and multiple-nest territories for all five diurnal focal species. For all these species except Ferruginous Hawks, the maximum number of known alternative nests in a given territory was 4–6. For Ferruginous Hawks, our estimate of the maximum number of "potential" alternative nests within a given territory area is confounded by uncertainties about histories of origin and use. Only three known territories currently are associated with more than seven alternative nests. In each of these three cases (numbers of extant nests ranging from 11–17), all of the assigned nests are located in relatively contiguous bands of similar habitat (e.g., arrays of scattered junipers and/or suitable rock outcrops) and with the overall distributions of nests such that identifying logical breaks that may comprise separate territories is difficult. That said, in each case the overall spatial extent of the nest arrays is such that at least two, if not three, active nests could easily be situated among a given array with inter-nest spacing equivalent to or greater than the smallest documented spacing of active nests observed elsewhere in our study area. Our sense is that these areas may represent historical nesting areas that previously supported higher nesting densities, but for the past decade have seen comparatively limited use due to the drought and potentially other factors.

Compared to the other species, Swainson's Hawks are known to much more routinely build new nests each year, with a review indicating that >50% of nests were freshly built across three different studies (England et al. 1997). Moreover, their nests often are less robust and much flimsier than those of eagles and the other buteos, such that they often do not remain intact for very long if not reused and refurbished (JPS personal observation), and unlike the eagles and other buteos, Swainson's Hawks do not build or refurbish more than one nest per year (England et al. 1997). Previous literature does not provide, however, any comparative data on numbers of alternate nests within Swainson's Hawk territories, perhaps in large part because individual nests are relatively ephemeral and alternating use of different nests within a territory area is relatively uncommon. Among 42 Swainson's Hawk territories to which we have assigned more than one alternative nest, 11 (26%) have involved repeated use (across years) of a given nest with another used in an intervening year.

Our data on numbers of alternate nests within Golden Eagle territories generally match up well against data from previous studies, which suggest a range of 1–14 nests/territory but with 2 or 3 most typical (Kochert et al. 2002). In our study, 38% of the known territories contained a single nest, 47% contained 2–3 nests, and 15% contained 4–6 nests. Additionally, our estimate that 62% of territories contained at least one alternate nest fits well within the range of estimates (52%, 56%, and 100%) from three other nearby (Utah, Montana, and Idaho) studies highlighted in Kochert et al. (2002). Similarly, Keller (2006) reported as many as 12 nests per active territory in his north-central Utah study area, with an overall average for 2006 of 4 nests per active territory, 90% of 100 active territories containing at least one alternate nest, and 72% containing 2–5 nests.

Our data on use of alternate nests by Prairie Falcons appears to suggest a notable variant compared to previous studies (as reviewed in Steenhof 1998). Studies in Idaho, Wyoming, and Colorado all suggested that nesting birds tend to use different sites in successive years if alternatives are available. In our study, 59% of the known and extant (as of 2007) territories involve only a single nest site; 46% of these (26 territories) supported more than one active nest during the study (12 twice, 7 three times, 4 four times, and 3 five times); and among the latter 81% of the cases involved repeat nesting in consecutive years for up to five years in a row. Moreover, in a majority of such cases, apparently suitable alternative nesting sites were readily available nearby, but were not used. Among the remaining 30 territories for which we have documented alternate nest sites, 50% have supported nesting in consecutive years at the same site, for up to six years in a row.

Temporal and Spatial Patterns of Territory Activity

Our focal species often (>35% of the time) used the same nest or burrow for more than one year in a row, and all five primary diurnal species used some individual nests for ≥5 consecutive years. This suggests that these species exhibit relatively high fidelity to individual nest sites in this study area. We also found, however, that several to many years could pass between two nest starts at the same nest. We documented gaps between successive nest starts of up to 6 years for the Golden Eagle and Red-tailed Hawk, 5 years for the Swainson's Hawk and Prairie Falcon, and 4 years for the Ferruginous Hawk and Burrowing Owl. Moreover, given the limited duration of our overall survey period (10 years) and the fact that most (76%) of the nests involved in these calculations were monitored for ≤7 consecutive years, these values easily could be underestimates. In fact, at least for Ferruginous Hawks, we know 4 years is a substantial underestimate, because there are many nests in the study area that we know were built and used prior to 1998 but definitely were not used since then until 2006 and 2007 when several otherwise perennially inactive territories once again attracted nesting birds to existing nest sites. Regardless, we found that more than three years routinely passed between successive nest starts at given sites, which has implications for land managers seeking to provide adequate protection to raptor nests in the landscape.

Calculations concerning territory spacing should not be used to directly infer relative territory or home-range size, because territory spacing is more likely a function of habitat and substrate availability, was based on territory centers, not activity locations, and does not address actual space use within the territory. The reported values for minimum spacing of territories do suggest, however, thresholds in each species' tolerance for same-species neighbors. For example, the smallest within-species, nearest-neighbor distances for Golden Eagle, Ferruginous Hawk, and Prairie Falcon territories were ~700–800 m, whereas the minimum spacing for Red-tailed Hawks was ~500 m and for Swainson's Hawks only ~200 m (Table 9). In addition, inter-territory spacing of raptor nests is potentially insightful to researchers searching for alternate nests within a given territory. Our results suggest that alternate nests of each of the relevant focal species may be found very close together (<20 m apart), but were on average 300–600 m apart. Alternate nests of the Golden Eagle, Red-tailed Hawk, and Prairie Falcon occasionally were located very close together (<10 m apart) in situations where nests were placed on the same cliff face or outcrop. This reinforces the need to carefully search for all nests in an area, and not just assume that, because you have found one nest, it necessarily precludes the existence of others in the immediate vicinity (e.g., on opposite sides of the same outcrop and not visible from the same vantage point).

We estimated that the overall density of raptor territories occupied at least once during the survey period was 4.11 territories per 50 km², and that the study-area-wide territory densities of individual focal species (excluding the Peregrine Falcon) ranged from 0.41–0.83 territories per 50 km². In central Utah, Smith and Murphy (1973) documented densities of ≥1 active nest per 50 km² for Golden Eagles, Ferruginous Hawks, Red-tailed Hawks, and Burrowing Owls (note that our density estimates are based on all territory locations and would be even lower if restricted to active nests), but much lower densities (0.2–0.5) of active Swainson's Hawks and Prairie Falcons. Kochert et al. (2002) summarize data from a variety of other Golden Eagle studies in terms of amount of area per nesting pair, indicating a range of values from 29–252 km^2/pair, which roughly translates to 0.2–1.7 breeding pairs per 50 km^2. Estimates from nearby southwest Idaho (0.75) and Wyoming (0.83) fell in the middle of this range, but the low value derived from a study in Nevada. Our average density value for this species (0.65 territories/50 km^2) falls within the range but, when discounted by the fact that only 43–68% of the territories were active in a given year (Table 13), falls toward the lower end of the range. Steenhof (1998) summarizes density estimates from other study areas similar to ours (scattered cliff-nesting habitat in Montana, North Dakota, Utah, and Colorado) of 0.27–0.53 breeding pairs/50 km^2. Again, our estimated value of 0.51 territories/50 km^2, with 45–55% of these active in a given year falls at the bottom of this range.

Olendorff (1993) summarizes annual density estimates from a variety of other Ferruginous Hawk studies and documents a broad range of variability in estimates of area per breeding pair. The range of estimates recorded from several different studies in Utah during 30 study years, including those of Smith and Murphy, fell below 1.0 pair/50 km^2 a little less than half the time, but dropped to the level of our study-wide estimate of the total density of territories, whether active or not (0.41), in only 23% of the study years. This clearly suggests that our study area supports a relatively low density of nesting Ferruginous Hawks, especially given that in any given year of our study only 20–46% of the known territories supported active nests. England et al. (1997) summarize nesting-density estimates from a variety of other Swainson's Hawk studies and again document a very broad range of values up to as high as roughly 60 pairs/50 km^2 in central California; however, estimates from interior locations similar to our study area ranged much lower (0.15–0.65 pairs/50 km^2) and bracket our study-wide estimate of 0.41 territories/km^2 with 42–71% active in any given year. Preston and Beane (1993) summarize density estimates from a number of other Red-tailed Hawk studies and again document a very broad range of densities from roughly 1–38 breeding pairs/50 km^2, which, given our estimate of 0.66 territories/50 km^2 and 47–66% active in a given year, clearly suggests that our study area supports a comparatively low overall density of nesting Red-tailed Hawks.

Overall raptor territory densities were relatively high in the Grassy and Lakeside Mountains region, primarily reflecting relatively high densities of Burrowing Owls, Prairie Falcons, Golden Eagles, and Ferruginous Hawks. Weighting territory densities by proportional activity across survey years suggested, however, that actual nesting activity was lower than average in this region for each of the species discussed, with the exception of Golden Eagles in the northern section of the region (the most remote portion of the region). Because this region is situated closer to the Wasatch Front metropolitan area than any other portion of the study area and lies in close proximity to I-80, the major transportation corridor through the region, it supports a relatively high level of recreational activity (primarily OHV and shooting activity), as well as substantial livestock (mostly sheep in this area) grazing. The area also is surrounded on two sides by an active military landscape where aircraft and bombing activities are common, and contains two major industrial facilities (a toxic waste storage facility and a magnesium extraction and processing facility), a recently added landfill, and a variety of mining (mostly historic) and quarrying sites. Thus, this region, in particular, may represent a situation where breeding raptors are attracted to the general characteristics of the overall landscape and over time have established a relatively high density of nesting territories, but then tend to experience a high degree of human-related disturbance that results in relatively inconsistent nesting activity.

Among the focal species, only the Golden Eagle and Prairie Falcon are known to nest in the Newfoundland Mountains, and their territory densities are relatively high in this area; however, both exhibited below-average proportional activity in this region. Similarly, both species are nearly the exclusive occupants of the Silver Island Mountains, but again at least Golden Eagles experienced relatively low proportional activity levels in this region. The lack of other focal species and the generally lower activity levels of Golden Eagles and Prairie Falcons in these areas likely reflect the fact that these ranges are virtual islands within the study area (i.e., a relatively thin, largely remote mountain chains, completely surrounded by sparsely vegetated salt desert scrub and playa/wash habitats) and are particularly rugged and xeric environments. As our ordination analysis confirmed (Figure 13), these two species are the most likely among our focal species to occupy areas with a high abundance of rocky, cliff and canyon habitat, so their unique occurrence in both ranges is not surprising. Clearly, though, our results suggest that the relative aridity, lack of productive vegetation communities, and overall ruggedness of the landscapes result in a relatively harsh environment that likely supports relatively low prey abundances and therefore relatively low overall nesting activity levels of these species.

Overall, proportional activity at focal species' territories appeared to decrease from north to south, likely reflecting the general north–south trend of decreasing elevation and moisture across the study area. Graphical inspection of proportional territory activity also suggested particular hot spots of territory activity for all raptors and focal species (see Appendix C). Raptor activity appeared generally high in the Grouse Creek Valley and on the other side of the Grouse Creek Mountains near Prohibition Springs, with comparatively moderate and lower activity levels elsewhere in the study area. This pattern primarily reflects concentrations of buteo activity, with all buteos absent from the Newfoundland Mountains, only a few Red-tailed Hawks located in the Silver Island Mountains, and Swainson's Hawks entirely absent from the Grassy and Lakeside Mountains. In contrast, aside from being uniquely represented in the Newfoundland Mountains, Golden Eagle activity was highest along the north end of the Grassy and Lakeside Mountains region, and Prairie Falcon proportional activity levels were highest in the Red Dome and Wildcat Hills areas and lower and spotty elsewhere in the study area. Finally, Burrowing Owl occupancy rates were highest between the Matlin Mountains and Baker Hills and northeast of the Pilot Range, spotty elsewhere, and entirely lacking in the Newfoundland Mountains. The relatively high buteo densities and activity levels observed in the Grouse Creek Valley almost certainly reflect the presence of extensive irrigated pastures and hayfields in close proximity to pinyon-juniper habitats suited to nesting. Such habitats are undoubtedly relatively rife with rodents, snakes, and other suitable prey due to the augmented moisture and nutrient conditions. As discussed previously, the association between Swainson's Hawks and agriculture is well known (England et al. 1997) and Red-tailed Hawks have been documented to do well in close association with human environments (Stout et al. 2006). Ferruginous Hawks also are known to be attracted to agriculture when it is not a dominant component of the landscape (Schmutz 1989) and when it is in close proximity to nesting habitat (Wakeley 1978).

Both proportional annual occupancy and activity levels remained relatively high and stable for Golden Eagles, Red-tailed Hawks, Swainson's Hawks, and Prairie Falcons from 2001–2007 compared to Ferruginous Hawks. This may reflect greater sensitivity to drought conditions (i.e., lowest in 2002, near the height of the drought, and highest in 2005, the wettest survey year) and/or a greater degree of adaptive nomadism among Ferruginous Hawks in response to variable climatic/habitat conditions. A previous study in central Utah documented variation in annual numbers of Ferruginous Hawk pairs present and nesting ranging from 43% in low prey years to 89% in high prey years (Smith and Murphy 1979). Although we documented an overall lower range of values for proportions of active territories (~20–50%), the range of variability in the annual figures was more similar. This level of variation in nest-initiation rates is not unique to Ferruginous Hawks, however. For example, Golden Eagle activity levels are known to fluctuate to even greater degrees (~30–100% of pairs nesting) in response to cycles of prey availability (Steenhof et al. 1997, McIntyre and Adams 1999, Keller 2006). This suggests that a relatively unique combination of factors influenced Ferruginous Hawks in our study area and caused their activity patterns to differ markedly from the other species. In compiling his review of the species' ecology and status, Olendorff (1993) noted that northern Utah was one of the few areas where the species was clearly experiencing a distinct decline. Perhaps the difference in pattern for this species compared to our other focal species reflects a comparatively marginal, longer-term status in the region, whereby variation in annual activity levels is greater because transient or young breeders are attracted to the area only periodically when conditions are especially good.

The apparent decline in Burrowing Owl proportional occupancy likely reflected primarily our burrow-centric approach and low re-occupancy of previously used burrows. We considered each burrow an independent entity due to the inherent difficulty of assessing the territory dynamics of this semi-colonial species. Although Burrowing Owls commonly re-use traditional nesting areas, they often do not use the same burrow from year to year (Haug et al. 1993, Dechant et al. 2003a). As a result, monitoring individual burrows alone will necessarily lead to apparent declines in burrow occupancy. For example, monitoring historical burrows in southwest Idaho led to an apparent decline in occupancy from 42% to 11% in 3 years (Lehman et al. 1998).

Otherwise, the temporary dips in territory activity exhibited by most species in 2003 during the peak drought year and the subsequent rises in occupancy shown by most species in 2005 during the wettest year clearly suggest weather-related influences. Other evidence in the literature of weather affecting rates of territory occupancy and activity is scarce for our six focal species; however, winter severity is known to affect the percentage of Golden Eagles that lay eggs in Idaho (Steenhof et al. 1997) and it is well known that weather often influences at least the nest success and productivity of most of the species (e.g., Stinson 1980; Gilmer and Stewart 1984; Squires et al. 1991; Haug et al. 1993; Steenhof et al. 1997). The slightly delayed 2006 peak in Golden Eagle annual activity may have been the result of a lag effect of the relatively wet, mild conditions that occurred in 2005. That is, the moisture that arrived in 2005 may have produced vegetation changes that year that produced a greater abundance of prey during the following nesting season. Unlike all of the other focal species, which tend to focus their foraging on smaller, more fecund birds and mammals, Golden Eagles are strongly dependent on jackrabbits for prey and it simply may have taken longer for their populations to rebound following the return of moister conditions. Conversely, Red-tailed Hawks were unusual in showing relatively high occupancy and activity levels in 2003 during the height of the drought, with their activity levels only slightly higher in 2005. Reasons for this difference are uncertain but may reflect the species being much more of an adaptable generalist than the other focal species, which may have allowed the red-tails in the study area to persevere better during the drought by taking greater advantage of novel food resources.

Nest Success and Productivity

The generally low nest-survival values for 2001 likely reflect, at least partly, the influence of low and probably non-representative sample sizes; i.e., *n* equal only 6–19 observation intervals per species despite our having monitored 2–5 times more nests than that for all species except Ferruginous Hawks (Table 13). Estimates of apparent nest success, biased as they may be, indicated similar or higher values in 2001 compared to 2002 for all species. Furthermore, the nest survival estimates for Ferruginous Hawks suggested a strong increasing trend from 2001–2006, with a slight drop in 2007 (Figure 9), whereas estimates of apparent nest success varied from only 75–100% and showed no distinct trend across years. For other species, however, the patterns of interannual variation in estimates of nest survival and apparent nest success were much more similar, suggesting a unique problem with regard to the data for Ferruginous Hawks. One likely possibility is that the numbers of Ferruginous Hawk nests active and monitored in the study area each year were much lower than for all other species except in 2006 and 2007. This means that any loss of observation intervals due to insufficient monitoring detail, especially when a nest was eliminated entirely from consideration, likely had a much greater impact on the representativeness of the analyzed data than was true for the other more common breeders. Whether or not this imparted a greater or lesser bias to the data than using apparent nest success as the metric of choice is unknown, but again the unique, radical difference in indicators from the two methods suggests that some degree of middle ground most likely is the accurate picture.

Nest survival peaked in 2006 for the Golden Eagle, Ferruginous Hawk, and Prairie Falcon. This suggests that, unlike Golden Eagles, the latter two species appeared to respond relatively quickly to a wet year by immediately nesting in proportionately greater numbers; however, similar to the case for Golden Eagles, there appeared to be at least a 1-year lag between the onset of wetter conditions and improvements to overall landscape productivity sufficient to noticeably improve the chance of nest survival for these species.

On the surface it appears potentially anomalous that no species appeared to experience particularly low nest survival or per nest productivity during the peak drought year of 2003. Here it is imperative that we consider other metrics in combination with estimates of nest survival and per nest productivity to render accurate insight. For example, three species that showed relatively high nest survival and per nest productivity in 2003 (Golden Eagles, Prairie Falcons, and Swainson's Hawks) exhibited relatively low overall territory activity that year. A possible explanation is that during extreme weather or low prey years, such as 2003, only the most capable, experienced breeders are able to nest successfully, resulting in lower overall nesting activity but higher average nest success and per nest productivity because relatively inexperienced and less successful breeders do not even attempt to nest. In contrast to the case for other species, the relatively high and stable nest-survival and productivity rates documented for Red-tailed Hawks again may reflect the species comparative adaptability in using a broad variety of habitats and prey species (Preston and Beane 1993). It is also noteworthy that Swainson's Hawks experienced a particularly substantial drop in nest survival, as well as to a lesser degree per nest productivity, in 2007 compared to the other diurnal species. This difference almost certainly reflects the combined influence of scorching heat and the later nesting characteristic of this species. The average laying date of Swainson's Hawks in the study area is roughly 1–2 months later than for the four other diurnal species (Table 14). The scorching heat that characterized the summer of 2007 and brought a major outbreak of wildfires did not commence in earnest until July. By that time, most nests of the other species had already successfully fledged their young and collectively experienced only moderate reductions in nest survival and productivity. In contrast, the Swainson's Hawks still had most of their brood rearing to do and both our crew's direct observations and the statistics themselves confirm that the chicks simply were unable to survive the heat stress and attendant reductions in prey availability that ensued.

Nesting Phenology

The overall average Golden Eagle laying date in our study from 2001–2007 was 2 March, with the annual averages ranging from 26 February–10 March (Table 14). A previous study conducted approximately 75 km south of our study area reported a similar grand average for 14 Golden Eagle nests of 7 March (Smith and Murphy 1973). Another study conducted in the Grassy and Lakeside Mountains area indicated a range of individual laying dates from 7 March through 6 April (Peterson 1988). Keller (2006), whose 30+ year study of Golden Eagles overlaps our study area in the Grassy and Lakeside Mountains region and then extends throughout a large area of central and north-central Utah (overlapping the previous Smith and Murphy study area), reported laying dates ranging from 16 January to 27 March in 2006, with peak activity from late February through early March. Other studies in nearby states have reported similar, overall-average laying dates of 5 March for southeastern Oregon, 25 February and 1 March for southwest Idaho, and 14 March for northeast Wyoming (as summarized in Kochert et al. 2002).

In our study, laying dates of Ferruginous Hawks, Red-tailed Hawks, and Prairie Falcons averaged about the same time (11–14 April) and five weeks later than for Golden Eagles, and Swainson's Hawks averaged roughly one month later than these species (9 May). Peterson (1988) reported similar average laying dates for Ferruginous and Red-tailed Hawks (12 April and 13 April, respectively), but a slightly earlier average for Prairie Falcons (5 April). In contrast, Smith and Murphy (1973) reported earlier ranges of average annual dates for Ferruginous Hawks (1–10 April) and Red-tailed Hawks (17 March–7 April), but later laying dates (20 April) for two Prairie Falcon nests monitored in a single year. Other previous studies of Red-tailed Hawks reported earlier average laying in Arizona (9 March; Mader 1978) and later average laying in Alberta (1 May; Luttich et al. 1971). In reviewing a variety of past studies, Olendorff (1993) suggested that, at latitudes from 38–49° N, Ferruginous Hawks typically lay eggs from 18 March – 12 May, with only those nesting in Alberta and Saskatchewan nesting noticeably later (2–3 weeks) than those farther south. A previous, broad-scale review of the nesting phenology of Prairie Falcons indicated a grand-average clutch-completion date of 18 April ± 10 days, with later nesting at higher latitudes and higher elevations (Williams 1985). For Swainson's Hawks, Smith and Murphy (1973) reported a range of laying dates (17 April–13 May) that encompasses our range of annual averages (6–12 May), but suggests overall slightly earlier timing, possibly reflecting the influence of a more southerly location. A review of other previous studies suggested earlier laying for Swainson's Hawks in central California (late March through mid-April), but similar timing from late April to late May across several other states at similar latitudes as our study (England et al. 1997).

For all five of the primary, diurnal focal species, egg laying occurred relatively late in 2001 and 2002, substantially earlier in 2003 during the peak drought year, continued to become progressively earlier through 2005/2006, and then began to backtrack again to later average dates in 2006/2007. This 7-year period is too short to draw definitive conclusions about potential long-term changes in nesting phenology (e.g., in response to increasing global temperatures), but laying dates of both Golden Eagles and Red-tailed Hawk were negatively influenced by year (i.e., earlier laying in later years). However, these relationships were potentially confounded by the earlier nesting documented during wetter nesting seasons, which were also more common in later years (Figure 11). That said, modeling of laying dates in relation to nest-site and climatic variables failed to reveal any significant climate relationships for Ferruginous and Swainson's Hawks, and nesting-season precipitation appeared as a significant predictor only in the model for Red-tailed Hawks. Our modeling suggested that Red-tail nesting was delayed following wet/snowy winters, but rather than suggesting further delays during wetter nesting seasons, laying tended to occur earlier when the nesting season itself was less drought-stricken. Our study also suggested that Red-tailed Hawks tended to lay eggs later at higher elevations, which again likely relates to the influence of heavier snow cover. Petersen (1979) previously found that Red-tailed Hawks in Wisconsin delayed nesting in proportion to the amount of snow cover present in February and March.

For earlier-nesting Golden Eagles, nesting-season precipitation was not a significant predictor of laying dates, likely because most eagles begin nesting before or near the beginning of the period we defined (March-June) for "nesting-season" precipitation. Instead, eagles tended to nest later at overall wetter sites and following colder winters, suggesting that heavy winter snow cover delays their nesting, probably because of the effect on prey availability. Keller's (2006) long-term study across a larger area of north-central Utah suggests that eagle laying dates tend to average earlier during years of higher prey availability. This does not appear entirely consistent with evidence from our study that suggested earlier laying as the drought progressed (Figure 11) and general prey abundance presumably declined; however, there may be a complicated dynamic operating here in that relatively dry winters, in general, likely afford the eagles earlier access to prey resources and that benefit conferred by the progressing drought may have offset the disadvantage of declining prey densities. The model results for Prairie Falcons suggested a similar relationship with average site precipitation; i.e., later nesting at wetter sites, again presumably reflecting the negative influence of snow cover on prey availability or at least accessibility.

Reasons for the lack of significant laying-date modeling results for Ferruginous and Swainson's Hawks are uncertain, but may relate to the fact that both of these species generally nest at lower elevations than the other species (also a good reason to expect no relationship between laying dates and nest-site elevation) and therefore may not be as affected by variation in winter snow cover. Both species exhibited roughly similar overall patterns of variation in average laying dates across years of the study, but greater overall variability than the other species. This suggests that the drought cycle did influence the nesting phenology of these two species during our study, but that other factors confounded that influence to a greater degree than for the other species and precluded significant climate effects in the context of our specific modeling exercise. One possibility for Ferruginous Hawks is the relative influence of variation in numbers of nesting pairs. Between 2001 and 2007, variation in the number of active Ferruginous Hawk nests was 21–200% greater than for any of the other focal species. It is well known that experienced avian breeders tend to nest earlier and more successfully than younger, less experienced breeders (Lack 1966, Newton 1979: 106), and that during lean years only the most experienced breeders tend to nest (Newton 1979: 122–123). Clearly, the latter factor easily could have contributed to the general showing of earlier nesting during the drought, when the numbers of active nests were down for all species. More importantly, greater variability in numbers of nesting pairs may well have translated to proportionally greater influence of breeder experience on the laying-date trends of Ferruginous Hawks and obscured potential climate relationships to a greater degree than for other species. In fact, as alluded to above, Olendorff's (1993) broad-scale review suggested that Ferruginous Hawk laying dates tend to vary a lot even within individual study areas and therefore the species does not show, for example, as strong a latitudinal gradient in laying dates as many other species.

HABITAT CHARACTERISTICS OF RAPTOR TERRITORIES

In general, raptor territories within the northwest Utah study area were more commonly in slightly higher and topographically more diverse areas than is characteristic of the landscape as a whole. This likely reflects the fact that most of the focal species largely avoided the lower elevation playa/wash and greasewood flats (generally devoid of nesting substrates for one thing) and instead nested in either the diverse cliff and canyon areas of the ridgelines, along foothill pinyon-juniper ecotones, or in the more mesic habitats found in the more northerly and generally higher-elevation portions of the study area. At the community level, nesting raptors in the study area also showed a general preference for nesting in areas with more big sagebrush and semi-desert shrub/grass vegetation and agriculture than is characteristic of the landscape as a whole. At somewhat the opposite end of the spectrum, however, raptor territories often contained proportionately more riparian and aspen vegetation than the landscape as a whole, despite the fact that these habitat types each occupy <1% of the total study area. In fact, the latter detail is consistent with the showing of a general preference for nesting in at least slightly higher-elevation areas, as these two habitat types generally occur only in elevated valleys and middle-to-upper ridgeline areas.

Not surprisingly, territories of the Golden Eagle and Prairie Falcon, both primarily cliff/outcrop nesters in our study area, were similar in regards to their habitat selection tendencies, with their territories tending to include more cliff and canyon habitat compared to other species. Their territories also tended to encompass more barren, playa, and semi-desert vegetation, but we suggest that the relationship with barren and playa habitats likely does not reflect a specific preference for such areas but instead may be an artifact of their nesting more frequently in the drier, more desert-like, southern portions of the study area along ridgelines that transition relatively quickly into playa and barren areas that are immediate extensions of the Great Salt Lake environs (e.g., except for a few Red-tailed Hawks in the Silver Island Mountains, they are the only species that inhabit the isolated and very dry Silver Island and Newfoundland Mountains regions).

Ferruginous Hawk territories were characterized by more agriculture, invasive grass/forbland, and big sagebrush shrub within 2-km of territory centers than was true for the landscape as a whole. Swainson's Hawk territories were similar, but showed an even stronger relationship with big sagebrush and agriculture, and lacked a strong association with invasive vegetation. The Swainson's Hawk, historically a bird of grassland vegetation, has adapted to foraging in agricultural areas planted with crops of similar height as native grasses (e.g., wheat and alfalfa; England et al. 1997). In contrast, previous studies suggest mixed relationships between nesting Ferruginous Hawks and agriculture (Howard and Wolfe 1976, Schmutz 1989, Bechard et al. 1990). Ferruginous Hawks may exhibit a "threshold" relationship with agriculture. Schmutz (1989) found that Ferruginous Hawk nesting densities in Alberta increased as the proportion of cultivation in the landscape surrounding nests increased to 30%, but decreased thereafter. Agricultural areas within our study area are a relatively small component of the overall landscape supported by a small human population, and tend to lie in close proximity to pinyon-juniper and other native vegetation types. Under such conditions, agricultural areas may provide attractive foraging habitat and abundant prey in close proximity to ideal nesting vegetation. For both the Swainson's and Ferruginous Hawk, vegetation height and density within agricultural areas may be the most important consideration, as both species apparently avoid foraging in dense, tall vegetation due to reduced prey vulnerability in such areas (Bechard 1982, Dechant et al. 2003b).

The apparent association of Ferruginous Hawks and invasive vegetation (primarily cheatgrass in our study area) has not been reported previously. Previous research on vegetation/prey relationships in southern Idaho suggests that areas dominated by cheatgrass support lower abundances of squirrels (*Spermophilus* spp.) and black-tailed jackrabbits (U.S. Department of Interior 1996, Steenhof et al. 2006). Additionally, ground squirrels may be more likely to go locally extinct in such areas due to the greater susceptibility of cheatgrass to drought (Steenhof et al. 2006). As with agriculture, the positive or negative reaction a species exhibits to cheatgrass vegetation is likely influenced by its coverage and juxtaposition to nesting habitat. Less extensive cheatgrass areas within the study area may provide relatively open foraging habitat where prey is still relatively available due to the close proximity of more prey-rich shrub cover. Alternatively, the apparent positive association with cheatgrass may simply be an artifact of where Ferruginous Hawks tend to nest, both historically and as a general tendency, because of other factors; e.g., they occupy a relatively specialized open-country niche where, probably to their detriment, cheatgrass tends to be most prevalent and is increasing in distribution at the expense of the native shrub-steppe habitat that once surrounded otherwise ideal nesting territories for the species.

Red-tailed Hawk territories contained more pinyon-juniper, montane sagebrush, and riparian vegetation, as well as more human development, than the landscape as a whole and in comparison to other species. Both riparian areas and areas of human development likely attracted Red-tailed Hawks more than other species because of the availability of relatively tall, commonly deciduous nest trees, which the species tends to prefer over shorter-stature substrates (Preston and Beane 1993). Human development areas, in particular, commonly contained the only tall trees found across much of the study area, including planted cottonwoods, elms, and other deciduous species. Evidence of more pinyon-juniper and montane sagebrush coverage within Red-tailed Hawk territories is consistent with the fact that this species nests across a relatively broad range of elevations that extend from the scattered, low-elevation fringes of foothill pinyon-juniper ecotones and stringers, where Ferruginous and Swainson's Hawks are more common, all the way up through and to the upper-elevation fringes of relatively extensive pinyon-juniper habitats that are interspersed with montane sagebrush and grassland meadows where they are able to hunt. In fact, our studies in adjacent portions of northeast Nevada where the average, landscape elevation is higher and a much greater portion of the lower-elevation areas is covered by mature, dense sagebrush, the distribution of nesting Red-tailed Hawks shifts from primarily the lower-elevation mixed juniper and shrub-steppe habitats to the upper fringes of pinyon-juniper habitats where open montane meadows are common and provide necessary foraging areas (unpublished data).

Burrowing Owl nesting areas tended to encompass more invasive grass/forbland vegetation (primarily cheatgrass) and mixed salt desert scrub within 2 km of burrows than the landscape as a whole. Burrowing Owls typically select for nesting relatively open areas with a clear view of surrounding habitat (Haug et al. 1993, Dechant et al. 2003a) and fire may create attractive nesting areas by reducing coverage of surrounding vegetation (Green and Anthony 1989). Rich (1986) also reported that Burrowing Owl nest sites contained more cheatgrass, compared to random sites, in southern Idaho. Mixed salt desert scrub vegetation generally is of lesser stature than sagebrush and greasewood vegetation, and may provide Burrowing Owls with a less obstructed view of their surroundings.

MODELLING LANDSCAPE CORRELATES OF TERRITORY ACTIVITY

Golden Eagles

Our results suggested that landscape, climate, and nest-site variables performed poorly (McFadden's ρ^2 or adjusted r^2 <5%) as predictors of Golden Eagle annual territory activity and nest productivity, and we do not revisit the overall interpretation of the modeling results here. We do note, however, that the top models for annual activity contained landscape variables measured at the average home range scale (3.0-km radius), whereas the productivity models contained landscape variables measured at the smaller study-area scale (0.5-km radius) and average home range scale, and that productivity was negatively related to invasive vegetation at both scales (we intentionally make special reference to the human-influenced landscapes types in this discussion). As previously discussed, areas with more invasive vegetation may have contained lower abundances of prey species, such as black-tailed jackrabbits (U.S. Department of Interior 1996). Jackrabbit abundance appears to be a primary driver of Golden Eagle reproductive output in Utah and Idaho (Smith and Murphy 1979, Bates and Moretti 1994, Steenhof et al. 1997, Keller 2006). We also note that the poor performance of Golden Eagle productivity models may have been partially due to the typically low variability in per nest productivity (especially per successful nest, as was modeled here) for this species due to typical production amounting to only a single fledgling rather than multiple fledglings as is more typical of the other species.

Nest-site variables accounted for a much larger 10% of the variation in Golden Eagle proportional territory activity, with activity greater at territories containing more nests. Various hypotheses exist to explain the function of alternate nests in raptors, although none has been tested empirically. An observational study of Bonelli's Eagles in Spain supported the nest-competition avoidance hypothesis (i.e., alternate nests allow a pair to move in response to disturbance or nest usurpation by another species) and ectoparasite-avoidance hypothesis (Ontiveros et al. 2008). In our study, it is unlikely that Golden Eagles would perceive other nesting raptors in the study area as competition, but territories containing more nests may have allowed greater nest shifting on an annual basis to facilitate ectoparasite avoidance. Alternatively, maintaining a suite of alternate nests may allow for shifting locations according varying climatic and nest-exposure factors or may simply serve as an insurance policy in case of nest destruction. For example, in one perennially occupied territory south of Grouse Creek Valley, the pair had been using one nest routinely but then a winter cliff fall totally removed that nest from the cliff. Despite this loss, they were able to immediately move to a nearby alternate nest the next spring and continue nesting successfully. Although the maintenance of alternate nests must have an evolutionary function to justify the effort they require, we also suggest that in our case, it is difficult to separate the cause and effect in the relationship. That is, proportional activity itself may have had a significant influence on the number of nests in a territory, given that more consistently active territories are afforded more time during which to "accumulate" nests, relative to less consistently active territories.

Climate variables also performed a bit better (McFadden's $\rho^2 = 9\%$) in the prediction of nest survival, suggesting that the probability of survival increased following cooler years and during wetter nesting seasons. Wetter conditions during the nesting season may have been correlated with increased vegetative biomass and prey availability. Previous research has suggested that increased winter severity can negatively influence Golden Eagle reproductive output (Tjernberg 1983, Steenhof et al. 1997), especially during periods of reduced prey abundance (Steenhof et al. 1997). In our case, however, although our laying-date analyses suggested that at least nest initiation was similarly affected by winter severity, the short duration of our study and occurrence of a severe drought cycle may have led to the apparently contradictory finding that increased nest survival followed cooler years as opposed to less severe winters.

Ferruginous Hawks

Similar to the Golden Eagle, top models of Ferruginous Hawk annual territory activity and productivity performed poorly (McFadden's ρ^2 or adjusted r^2 <6%), whereas models of proportional activity and nest survival were of greater value (McFadden's ρ^2 or adjusted r^2 of ~15–22%). The top models of annual activity and productivity contained landscape variables measured at the study-area scale (1.5-km radius) and upper-home-range scale (5.0-km radius), respectively. Annual activity was positively related to human development at the smaller study-area spatial scale, whereas productivity was negatively related to human development, disturbed land (somewhat mixed relationship though), and, to a lesser degree agriculture, but positively related to invasive vegetation, semi-desert shrub/grass, and mixed sagebrush shrub (somewhat mixed relationship though) at the larger upper-home-range scale. Landscape variables measured at the study-area scale (1.5-km radius) were able to explain up to 22% of the variation in proportional activity, and top models suggested that activity was greater at territories with less topographic diversity and less desert/flats vegetation (i.e., mixed salt desert scrub and greasewood flats) and marsh, but more invasive vegetation, semi-desert shrub/grass, human development, and water. The top nest-survival models, measured at the 1.5-km scale, also suggested positive associations with human development and disturbed land, but a negative association with invasive vegetation. The combination of indicators suggests to us that Ferruginous Hawk nesting activity in the study area is most concentrated in areas of relatively high human activity and coverage of invasive grass/forbland, but that this does not necessarily translate to consistent benefits in terms of nest survival and productivity. Relative to the contradictory relationships indicated for invasive vegetation (positive relationships with proportional territory activity and productivity, but negative with nest survival), if we assume that the negative relationship between nest survival is real and discount the apparent positive relationship with productivity (due to the poor performance of the productivity models), these contradictions may suggest an ecological trap (i.e., an inappropriate attraction to poor quality habitat; Gates and Gysel 1978). That is birds may be attracted to nesting in areas with apparently favorable open foraging habitat nearby (i.e., invasive vegetation), but prey abundance may be lower in these areas (e.g., see U.S. Department of Interior 1996, Steenhof et al. 2006), leading to decreased nest success. It also is possible that the apparently contradictory indicator for productivity (per successful nest) reflects the fact that poor overall nest survival translates to the only nests that succeed being those of experienced breeders whose productivity is, in general, relatively high.

We previously described Ferruginous Hawk territories as containing more agriculture and invasive vegetation compared to other raptor species, and we speculated that the relatively open nature of both vegetation types might provide attractive foraging habitat, particularly when they are not the predominant vegetation type in the larger landscape and are found in close proximity to potential nesting habitat (e.g., pinyon-juniper). Selection of less topographically diverse habitats is consistent with this species being an open-country specialist, and we already discussed why the apparent positive association with cheatgrass may be an artifact of landscape change and the species' preference for the lower-elevation, open landscapes that are rapidly being taken over by cheatgrass. Activity was lower at territories with more desert/flats vegetation probably due to lower vegetation productivity and potential prey in such areas compared to the much more mesic and productive landscapes the species also occupies in the study area near agricultural and irrigated-pasture habitats maintained by humans. The Ferruginous Hawk is touted as being relatively sensitive to human disturbance (Olendorff et al. 1993, Bechard and Schmutz 1995) with a tendency to nest farther from human activities compared to Swainson's and Red-tailed Hawks (Schmutz 1984, Bechard et al. 1990). Our results suggested a mixed relationship with human development and disturbed lands, with positive values accrued at smaller spatial scales surrounding the nest sites but negative effects accrued if such habitats comprised a substantial portion of the larger landscape. In our study area, the extent of human activity generally is limited and relatively uncommon irrigated hayfields and pastures clearly are a powerful draw for all three buteo species in this otherwise xeric landscape. Our results suggest though that there is a limit to how much such "disturbance" Ferruginous Hawks are able to tolerate and remain secure and productive in our study area.

Red-tailed Hawks

The best models of Red-tailed Hawk annual activity (Mc Fadden's ρ^2 = 8%), nest success (ρ^2 = 5%) and productivity (adjusted r^2 = 5%) all performed only marginally. Annual activity and productivity both were best modeled at the study-area/average-home-range scale (1.0-km radius). Both sets of models suggested primarily positive relationships with disturbed areas and mixed or montane sagebrush/grass habitats, and negative relationships with invasive vegetation. Annual activity was also positively related to coverage human development and riparian woodland/shrubland, but the productivity models suggested mixed relationships for these cover types. The top productivity model also suggested a relatively strong negative association with agriculture. The top nest-survival models contained landscape variables measured at both the upper-home-range scale (2.0-km radius) and smaller 1.0-km scale. Both scales suggested positive relationships with agriculture and the 1.0-km model indicated a positive relationship with human development. Landscape variables measured at the 1.0-km and 2.0-km scales accounted for a high proportion of the variance in proportional territory activity (35–36%). The overall suite of relationships indicated in these models presented some interpretation difficulties, perhaps reflecting the relatively flexible habitat usage of this species (Preston and Beane 1993). At both scales, however, activity was positively related to cover of human development and agriculture, and negatively related to cover of mixed sagebrush/grass and semi-desert shrub/grass, and the top (1.0-km) models also indicated a negative relationship with invasive grass/forbland. Thus, mostly positive relationships were indicated with regard to human development, agriculture, and disturbed habitats, whereas consistently negative relationships were indicated for invasive vegetation. Previous studies in northern Utah also reported a positive association between Red-tailed Hawk nest sites and agriculture (Platt 1971, Bosakowski et al. 1996), and we previously discussed the apparent tolerance of Red-tailed Hawks for human development. The negative relationship with invasive vegetation (cheatgrass) also is not surprising given higher proportional activity levels at higher elevations and the tendency of this species to nest in less-open/more-wooded areas or in human-dominated landscapes where agriculture and other mixed disturbed habitats are more prevalent.

Swainson's Hawks

Swainson's Hawk annual activity was best modeled with nest-site variables, but again the best model performed poorly (McFadden's ρ^2 = 3%), and the top nest-survival model, containing climate variables, performed only marginally (McFadden's ρ^2 = 7%). In contrast, nest-site variables were able to account for a high 26% of the variation in proportional activity, which was greater at more mesic and higher elevation sites, and at territories with more alternate nests. A variety of factors may contribute to the benefits of higher-elevation and more-mesic nest sites. In our study area, taller nest trees, which Swainson's Hawks often prefer, if available and not already occupied by Red-tailed Hawks, are found most frequently either at higher elevations (larger, mature junipers) or in relatively mesic areas along stream courses, around reservoirs, and around human settlements (cottonwoods, elms, large willows, etc.). Mesic sites almost certainly also offer relatively high prey abundances, and occupying relatively high-elevation sites may reduce competition with Ferruginous Hawks. The top productivity models also performed only marginally (accounting for 7–9% of variation in the data), incorporating landscape variables measured at the average-home-range (3.0-km) and upper-home-range (5.0-km) scales. At either scale, productivity generally was greater at nests surrounded by less desert/flats (greasewood, mixed salt desert scrub, playa/wash, etc.) and marsh, but more big sagebrush shrub and water, and the larger-scale models also indicated positive associations with higher-elevation aspen mix, montane sagebrush/grass, and mixed conifer habitats. Again, it is likely that desert/flats areas are less productive habitat for potential prey, whereas big sagebrush shrub habitats at lower elevations and montane sagebrush/grass habitats at higher elevations likely provide richer mosaics of shrub and grassland habitats that support higher densities of rodent, avian, and insect prey. At the smaller scale, productivity was also negatively related to invasive vegetation, whereas at the larger scale it was positively related to agriculture. We previously discussed the potential causes of decreased productivity in areas with more invasive vegetation (i.e., lower prey abundance; U.S Department of Interior 1996, Steenhof et al. 2006) for Ferruginous Hawks, as well as the well-known association between Swainson's Hawks and agriculture (England et al. 1997).

Prairie Falcons

As with all previous species, the best model of Prairie Falcon annual activity, containing nest-site variables, performed poorly (McFadden's ρ^2 = 5%). Nonetheless, they indicated higher activity at lower-elevation and more mesic sites. Productivity, best modeled at the 2.0-km and average-home-range (5.0-km) scales, also fared poorly (adjusted r^2 = 5–6%), and indicated a mixed relationship with agriculture at the smaller scale and a negative relationship at the larger scale. Productivity was also negatively associated with human development at both scales and with disturbed areas at the larger scale. In contrast to the poor performance of all other models, the proportional activity models again performed much better (accounting for up to 32% of the variance in the data), with nest-site variables most important for this species. Proportional activity was greater at territories with more nests and at sites with less topographic ruggedness in the immediate vicinity of the nest site. The latter suggests that, although Prairie Falcons frequently nest in relatively complex and rugged cliff and canyon habitats, they may prefer sites that afford relatively broad-scale visibility from their eyries.

The best nest-survival models also performed reasonably well (McFadden's $\rho^2 = 13\%$) and reflected complex mixes of landscape variables measured at both the average-home-range (5.0-km radius) and upper-home-range (10.0-km) scales. Both of the top 10-km landscape models indicated a negative association with elevational diversity, and the overall suite of landscape models consistently indicated negative associations with mixed salt desert scrub and mixed sagebrush shrub, but mixed relationships for cliff/canyon, exposed rock, and barren habitats, depending on the spatial scale. The 5.0-km model indicated negative associations with the latter habitat types, whereas the larger-scale 10-km models suggested the opposite. This contrast appears to mimic the results of the proportional activity models in suggesting that the overall landscape in which the species nests typically is rife with cliff/canyon and other rocky habitats, but at a more localized scale Prairie Falcons in our study area appear to prefer areas within the broader landscape that are relatively open, canyon free, and less rocky. This may reflect benefits pertaining to both better foraging opportunities (more vegetated and open habitats likely contain more accessible prey) and an improved ability to maintain defensive vigilance around their nest sites. Contrary to the productivity models, the fourth-ranked 5.0-km nest-survival model also indicated a positive relationship with human development, as well as with invasive grass/forbland and greasewood flats. This suggests that, somewhat analogous to the case for Ferruginous Hawks, Prairie Falcons may be attracted for nesting to apparently favorable areas where the level of human development is relatively high and, in this case, may achieve reasonable nest success in such habitats but are unable to achieve high fledgling production. This may reflect either marginal foraging habitat or perhaps some aspect of human-related disturbance that precludes higher productivity (e.g., human activities cause the adults to remain more vigilant around their nest, which limits time spent foraging). Lastly, the complete absence of significant relationships in other models, but indication of an apparent positive association between Prairie Falcon nest survival and cheatgrass is difficult to explain, especially given the prevalence of negative associations in the nest-survival and productivity models for the four other diurnal species. One possible explanation is that Horned Larks (*Eremophila alpestris*) and Western Meadowlarks (*Sturnella neglecta*) are abundant in many mixed grassland areas where cheatgrass is relatively prevalent, and both of these species are well-known, important prey species for Prairie Falcons (Steenhof 1998), but are not utilized as routinely by the other species. That said, however, the complete lack of other significant relationships with invasive vegetation suggests a very tenuous association at best.

Burrowing Owls

Climate variables were the best predictors of annual occupancy for Burrowing Owls, but similar to all other focal species, the annual models performed poorly (McFadden $\rho^2 < 3\%$). Nonetheless, the top climate models suggested higher occupancy rates following overall warmer and wetter years, but a relatively cool, dry winter. This may reflect benefits following years of relatively high landscape productivity but only when combined with a winter climate (limited snowpack) that precludes excessive vegetation growth during the current nesting season; i.e., a combination that provides for overall good prey resources carrying over from the previous year, but limits grassland growth to a height favorable to nesting Burrowing Owls that require broad visibility around their burrows. The top proportional occupancy models, containing nest-site and landscape variables, performed better but still explained only marginal proportions of the variance in the data (8–11%). Nest-site variables suggested that proportional occupancy was greater at higher elevations and sites surrounded by less topographic ruggedness in close proximity to the burrow. Burrows at higher elevations may have been located in more productive habitat, but also may have been located in foothill areas that provided greater visibility across surrounding landscapes. Burrows located in less variable terrain likely provide owls with greater visibility of their surroundings, providing greater security at the nest and access to prey. Rich (1986) reported that burrows were generally surrounded by flat terrain within a 50-m radius in southern Idaho, and Burrowing Owls are known to nest in level to gently sloping areas surrounded by sparse vegetation (Haug et al. 1993, Dechant et al. 2003a). The landscape models included variables measured at both the study-area (1.0-km radius) and upper-home-range (1.5-km) scales, and consistently indicated positive associations with big sagebrush shrub and negative associations with invasive vegetation. One of the 1.5-km models also indicated a positive association with agriculture. The indication of a negative relationship with invasive vegetation contradicts the previous indication that Burrowing Owl burrows tended to be located in areas that contained proportionately more invasive vegetation than the landscape as a whole. Again, this may reflect an ecological-trap situation and the rapidly changing nature of the study area landscape due to increasing cheatgrass invasion. In other words, in this landscape the owls may be attracted to open shrubsteppe and grassland areas that contain a high proportion of cheatgrass, because on the surface such areas appear to represent suitable nesting habitat, but only to find that in fact they are relatively unproductive habitats and therefore the owls do not return to such areas on a regular basis. In fact, our observations suggested that the cheatgrass-dominated habitats used by some owls in our study area exhibited substantial variability from year to year in terms of general suitability for owl nesting. That is, during relatively dry years such habitats were well suited to owl nesting because the grass height was low, but in wet years the cheatgrass grew 2–3 times higher and obscured all possibility of visibility at burrow height. Moreover, other mixed shrub and grassland habitats in the study area that feature primarily bunch grasses are spatially diverse and therefore provide a variety of options under diverse growth conditions for the owls to find a suitable burrow location that also affords good visibility options. In contrast, cheatgrass ultimately grows in extensive and dense monocultures that, when tall enough, provide no possibilities for suitable visibility at the burrow.

CONCLUSIONS AND MANAGEMENT IMPLICATIONS

We stress that drought conditions dominated the period during which we monitored raptor nests in the northwest Utah study area, and that the trends in raptor territory activity we report here should be viewed within this context. Additionally, we used a simplified, static vegetation map to assess habitat characteristics of raptor territories and the influence of vegetation on territory activity, nest success, and productivity. Acknowledging these two caveats, our results have important implications for the monitoring and protection of nesting raptors and specifically for managers of lands supporting nesting Golden Eagles, Ferruginous Hawks, Red-tailed Hawks, Swainson’s Hawks, Prairie Falcons, and Burrowing Owls.

Our research highlights the importance of taking a territory focus when attempting to monitor or protect nesting raptors. That is, individual nests are not necessarily independent entities, but rather often belong to a larger complex of nests within a specific territory. We routinely documented multiple-nest territories for all five of our focal, diurnal species. A lack of activity at a single nest certainly does not preclude activity elsewhere in the territory. Special attention must be paid to other available nesting substrates near any individual nests one may discover. Based on our work, we suggest that searches for alternate nest sites routinely extend to a radius of at least 1 km, but much larger distances often separate individual nests within Golden Eagle territories. We provide detailed recommendations for monitoring raptor nests in Smith et al. (in press). Although this document was specifically written to guide monitoring in relation to oil and gas development activities, the protocols are widely applicable to most raptor monitoring programs.

Focal raptor species in the northwest Utah study area commonly exhibited fidelity to specific nests, and therefore, the knowledge of previously active nest sites can be used to guide initial efforts to locate nesting birds. A lack of activity at a particular nest, however, should not be used to discount the possibility of activity in the general area. Additionally, our results revealed that three or more years commonly passed between documented nesting activities at individual nests. The Utah Bureau of Land Management “Raptor Best Management Practices” recommend extending spatial protection to recently active nests during the breeding season, but suggest that nests inactive for three consecutive years be considered abandoned and exempted from all protections. In contrast, the Utah office of the U.S. Fish and Wildlife Service previously recommended protecting inactive nests for a minimum of 7 years (Romin and Muck 2002) and subsequently summarized data to support this recommendation (U.S. Fish and Wildlife Service 2006). Based on our results, we suggest that five years of protection may be a reasonable compromise for the focal species in this study; however, adopting this criterion would still afford the possibility of neglecting many nest sites that might otherwise be used again under suitable circumstances, even after intervals that extended well beyond 7 years. ***For confirmed multiple-nest territories, we further advocate that protections be extended equally to all nests in the territory based on the most recently active nest; i.e., a nest that has been inactive for >7 years should not be considered expendable if it belongs to a more recently active territory.***

Within the northwest Utah study area, we found that territory activity appeared to decrease from north-to-south, likely following a decreasing elevation and moisture gradient across this area. General raptor activity was especially high in Grouse Creek Valley and near Prohibition Springs, likely due to the combinations of habitats available in these areas and especially the relative prevalence of irrigated and/or naturally mesic environments found therein. The Salt Lake Field Office of the BLM and the UDWR should be aware of the importance of these areas to raptors and, in particular, nesting Ferruginous, Red-tailed, and Swainson's Hawks. Considering the relatively high proportion of private lands in these areas, local landowners should also be educated about the significance of their lands to breeding raptors.

Despite drought conditions throughout much of the study, territory occupancy and activity were generally high for Golden Eagles, Red-tailed Hawks, Swainson's Hawks, and Prairie Falcons across years, suggesting that the drought cycle did not substantially affect the general nesting tendencies of these species in the study area. We did detect, however, apparent correlations between annual trends and climatic conditions. In particular, all focal species exhibited some type of positive response (i.e., increased occupancy, activity, nest success, and/or fledgling production) to the wettest year (2005) and/or following year. The prolonged or delayed responses to such conditions that we observed for most species suggest that the potential benefits of wetter conditions (i.e., greater vegetative biomass and prey abundance) are not necessarily restricted to the year in which they occur.

Our work in northwest Utah highlights the difficulties of adequately monitoring Burrowing Owls with typical, community-level raptor nest-monitoring protocols. Due to their colonial and subterranean habits, the territory dynamics of Burrowing Owls are difficult to establish without prolonged observations and marking individuals, and as a result we were forced to consider each burrow as an independent unit rather than being able to identify individual territories as containing a series of alternate nest sites. This undoubtedly was at least partially responsible for the declining occupancy trends we reported for this species across survey years, as individuals likely switched between burrows over time. We suggest that, in the absence of a more advanced understanding of individual territory dynamics, surveyors focus on the overall occupancy, activity, etc. of entire "burrow complexes" (i.e., spatially clumped burrows distinct from other burrow clumps).

The average egg laying date for Golden Eagles in the northwest Utah study area from 2001–2007 was 2 March, while Ferruginous Hawk, Red-tailed Hawk, and Prairie Falcon laying dates averaged about five weeks later (11–14 April), and the average Swainson's Hawk laying date occurred considerably later on 8 May (also typical timing for Burrowing Owls). The laying dates we report do not vary in any consistent manner from previous studies conducted within or near the study area. Although it did appear that nesting was initiated later during the earlier survey years, and earlier in 2003–2006, the short duration of this study and the potential confounded relationship between moisture conditions and survey-year preclude inferences from this result. That is, nesting season moisture, greater in later years, was also related to earlier nesting.

Human-influenced landscape types, particularly, agriculture, invasive vegetation, and/or human development were identified as influential to each of the focal species according to at least one metric of nest activity, survival, or productivity metric. In particular, the complicated relationships indicated for Ferruginous Hawks and Burrowing Owls in relation to invasive cheatgrass appear to warrant further research. The territories of both species contained more invasive vegetation than the general study area, but modeling suggested that within these territories, those that contained more invasive vegetation contained less successful nests (Ferruginous Hawk) or were occupied for a lower proportion of survey years (Burrowing Owl). We suggest that relatively extensive areas of cheatgrass, commonly established by fire, may appear to provide attractive foraging areas because they are relatively open, but previous studies suggest that such areas contain lower prey abundances (U.S. Department of Interior 1996, Steenhof et al. 1996).

In recent years, scientists have increasingly recognized the need to consider multiple scales when attempting to understand biological patterns (e.g., see O'Neill et al. 1986, Kotliar and Wiens 1990) and have concluded that no single best scale of research exists (Levin 1992). Similarly, our results suggest that individual species from the same group (e.g., raptors) do not necessarily respond to landscape patterns at the same scale, at a single scale, or consistently across scales. Rather than selecting a single or multiple arbitrarily scales, it has been suggested that scientists use their knowledge of the study organism(s) of interest to help guide the selection of appropriate research scales (Levin 1992).

Finally, even the best of our models designed to describe the landscape correlates of raptor nesting activity in our study area explained substantially less than a majority of the variance in the datasets. Although not unexpected given the complexities of ecological systems, one major limitation of our work (a reflection of resource limitations) is the lack of information concerning prey abundance (Smith et al. in press). Other similar long-term studies that have also been able to rigorously monitor patterns of prey abundance clearly emphasize the relevance of such data for understanding the primary drivers of raptor ecology in similar regions (e.g., Steenhof et al. 1997, 1999). Thus, our final management recommendation is that to further advance our collective, detailed understanding of the ecology of the northwest Utah raptor community will require the addition of an extensive and rigorous program to simultaneously monitor prey abundance in the region.

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Appendix A. Standardized "nest location" data form.

BLM Nest # _______________	
GBRNS Nest # _______________	

HawkWatch International Nest Location Data Sheet

Species: ________________________ Status (active, inactive, unknown): ________________________

Territory Name (if known): ________________________

Observer(s): ______________________________ Date Discovered: ______________________________

7.5' Topo Quad Name: ______________________________ Topo Code: ________________________

Township: _______ Range: _______ Section: _______ Quarter Section: __________ Elevation: _______ (m)

GPS model used: ______________________ UTM Nest Coords: _____ Zone ____________E ___________N

UTM View Coords: ______________E ______________N Orientation / Distance to Nest: ________________

Land ownership (indicate owner/manager name when known):

Private: _____________________ State: _____________________ Federal: _____________________

Specific directions to nest site: ____

____

____

____

Map showing directions to nest site.

Digital Photos

Type	Camera	Photo#	Orientation
L1			
L2			
L3			
N			

General Description of Nest Site:

Substrate (e.g., cliff or outcrop [rock type], tree/shrub [species, live/dead], ground, artificial structure [type]):

____

Estimated height of substrate: _________(m) Estimated height of nest above ground: ________(m)

Nest type and location on substrate (e.g., stick nest in upper/lower canopy stick nest on/in ledge, pothole, or crevice; scrape on/in ledge, pothole, or crevice; stick nest on artificial platform mounted in tree; tree cavity; burrow; etc.):

____

Protection from weather (YES/NO; describe nature of protection, e.g., tree canopy, cliff backdrop, pothole/crevice, burrow, etc.):

____

Approximate compass direction of exposure to elements (wind, sun, etc.): ___________________________

Describe visibility and accessibility of nest (relative to obtaining accurate status/productivity data, possibility for banding or nestling exams, searching for prey remains, and accessibility for predators, etc.):

____

____

____

Nest size—indicate whether estimated or measured: ________________

Height (top to bottom)_______ Width (left to right)_______ Depth (back to front)_______ (meters)

Known or probable alternative nests within territory and associated nest #'s:

____

____

Standard description of habitat types and land uses within 1-km radius of nest using UDWR classification codes and estimates of percentages of each habitat type within area, and any additional notes about apparent habitat condition:

____

____

____

Additional notes about human activity within 1-km radius of nest (e.g., heavy road traffic, density of homes, recreational activities, etc.):

____

____

____

____

____

Miscellaneous Notes:

____

____

____

____

____

Appendix B. Standardized "nest history" data form.

HWI Raptor Nest History Data Sheet **Nest #______________** **Page ___ of ___**

Date (mm/dd/yy): ________________ Observer(s): ____
Observation Begin Time: ______________ End Time: ______________ (24-hr clock, Local Standard Time only)
Species: __________________________ Time to confirmation of active status: ________________________
Status (unknown, inactive, occupied territory, occupied inactive territory, courtship/nest building, incubating, nestlings, fledglings, failed): ____
\# Dead Eggs: ______ # Live eggs: ______ # Dead young: ______ # Live young: ______ Nest poled? Y / N
Estimated Ages of Young (days): ______________________________________ # Banded: __________
Basis for age of young (describe plumage and/or behavior): ____

Description of adult activity: ____

****

Date (mm/dd/yy): ________________ Observer(s): ____
Observation Begin Time: ______________ End Time: ______________ (24-hr clock, Local Standard Time only)
Species: __________________________ Time to confirmation of active status: ________________________
Status (unknown, inactive, occupied territory, occupied inactive territory, courtship/nest building, incubating, nestlings, fledglings, failed): ____
\# Dead Eggs: ______ # Live eggs: ______ # Dead young: ______ # Live young: ______ Nest poled? Y / N
Estimated Ages of Young (days): ______________________________________ # Banded: __________
Basis for age of young (describe plumage and/or behavior): ____

Description of adult activity: ____

****

Date (mm/dd/yy): ________________ Observer(s): ____
Observation Begin Time: ______________ End Time: ______________ (24-hr clock, Local Standard Time only)
Species: __________________________ Time to confirmation of active status: ________________________
Status (unknown, inactive, occupied territory, occupied inactive territory, courtship/nest building, incubating, nestlings, fledglings, failed): ____
\# Dead Eggs: ______ # Live eggs: ______ # Dead young: ______ # Live young: ______ Nest poled? Y / N
Estimated Ages of Young (days): ______________________________________ # Banded: __________
Basis for age of young (describe plumage and/or behavior): ____

Description of adult activity: ____

****

Date (mm/dd/yy): ________________ Observer(s): ____
Observation Begin Time: ______________ End Time: ______________ (24-hr clock, Local Standard Time only)
Species: __________________________ Time to confirmation of active status: ________________________
Status (unknown, inactive, occupied territory, occupied inactive territory, courtship/nest building, incubating, nestlings, fledglings, failed): ____
\# Dead Eggs: ______ # Live eggs: ______ # Dead young: ______ # Live young: ______ Nest poled? Y / N
Estimated Ages of Young (days): ______________________________________ # Banded: __________
Basis for age of young (describe plumage and/or behavior): ____

Description of adult activity: ____

Nest condition (poor, fair, good, excellent, gone, collapsed, burned, etc.):

Date				
Condition				

Comments____

Human activities:

Date	
Activity	
Vehicle Types	
# of People/Vehicle	

Date	
Activity	
Vehicle Types	
# of People/Vehicle	

Comments with observation dates and times, please record any signs of non-observed human activity and any bird reactions:

Habitat Condition and Changes (Please record developing conditions and changes to habitat in nest area such as fire or clearing):

Prey Observations (for each potential species observed):

At Nest:

Date	Species	Abundance or #	Remains	Comments

General observations of prey distribution and abundance around nest area, and notes about raptor foraging/feeding in area:

Appendix C. Graphical illustrations of the densities of raptor territories in northwest Utah for six focal species and all raptor species combined.

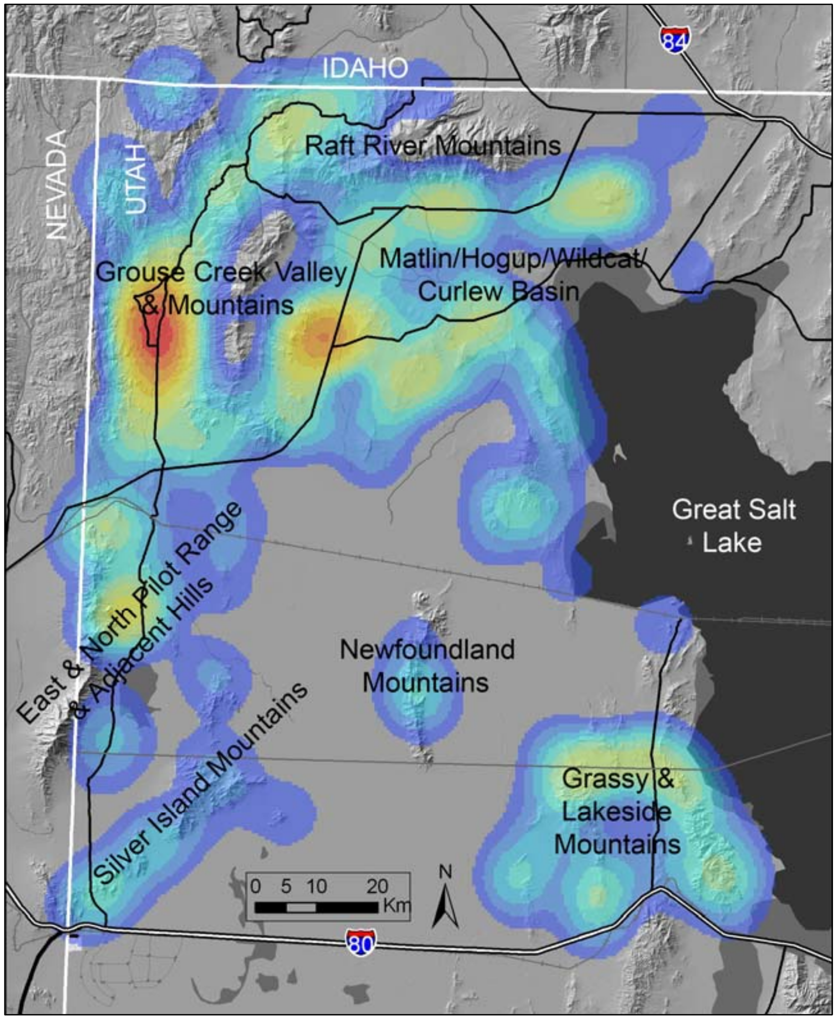

Figure C1. Density of all raptor territories in the northwest Utah study area surveyed consecutively for ≥5 years and weighted by proportional activity (i.e., nest starts) across survey years. Darker blue areas represent lower densities of activity, while darker red areas represent higher densities.

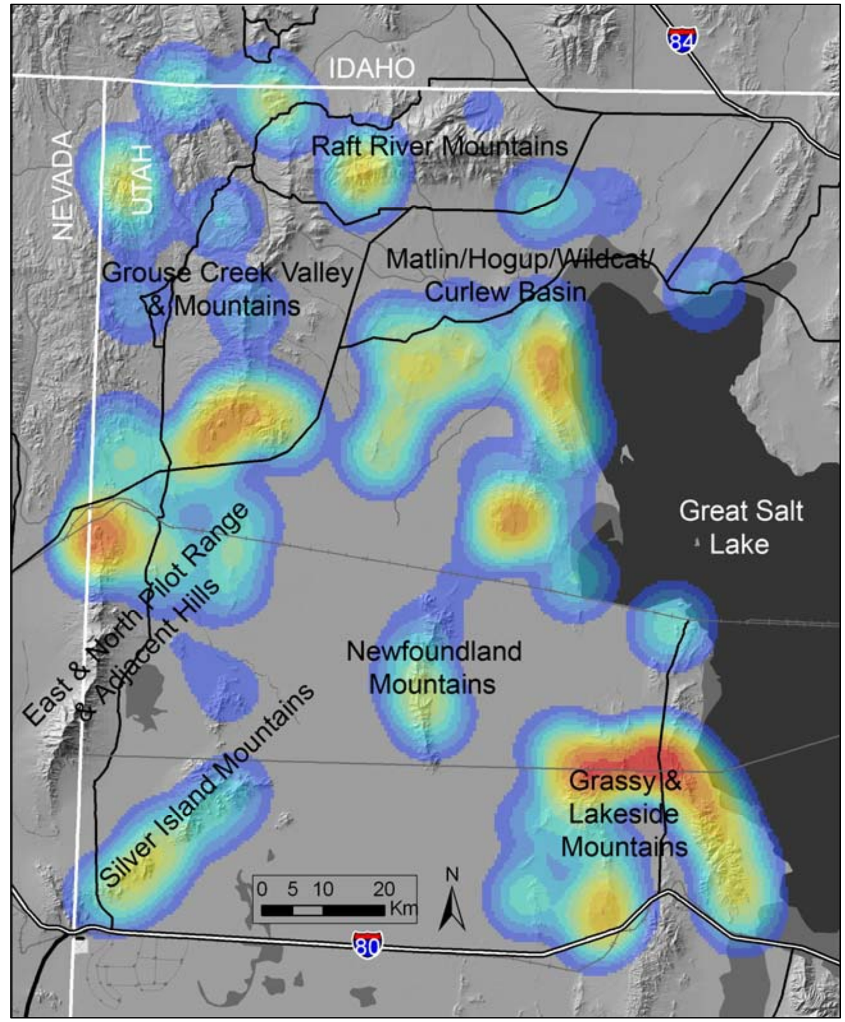

Figure C2. Density of Golden Eagle territories in the northwest Utah study area surveyed consecutively for ≥5 years and weighted by proportional activity (i.e., nest starts) across survey years. Darker blue areas represent lower densities of activity, while darker red areas represent higher densities.

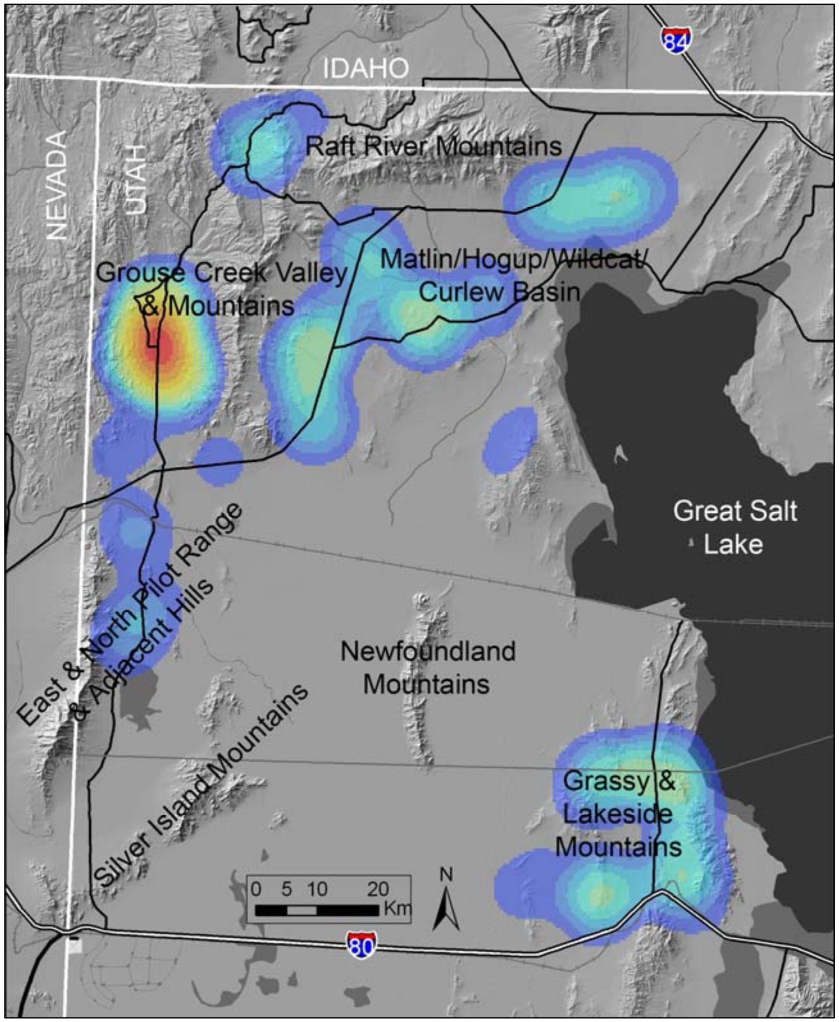

Figure C3. Density of Ferruginous Hawk territories in the northwest Utah study area surveyed consecutively for ≥5 years and weighted by proportional activity (i.e., nest starts) across survey years. Darker blue areas represent lower densities of activity, while darker red areas represent higher densities.

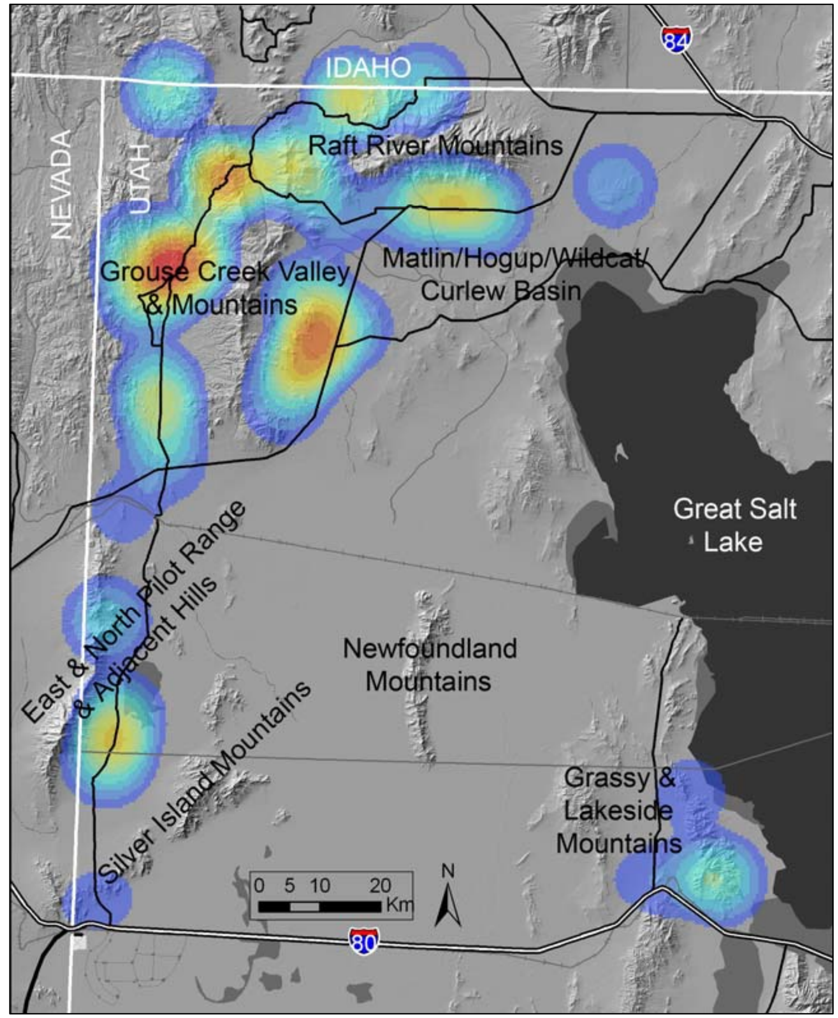

Figure C4. Density of Red-tailed Hawk territories in the northwest Utah study area surveyed consecutively for ≥5 years and weighted by proportional activity (i.e., nest starts) across survey years. Darker blue areas represent lower densities of activity, while darker red areas represent higher densities.

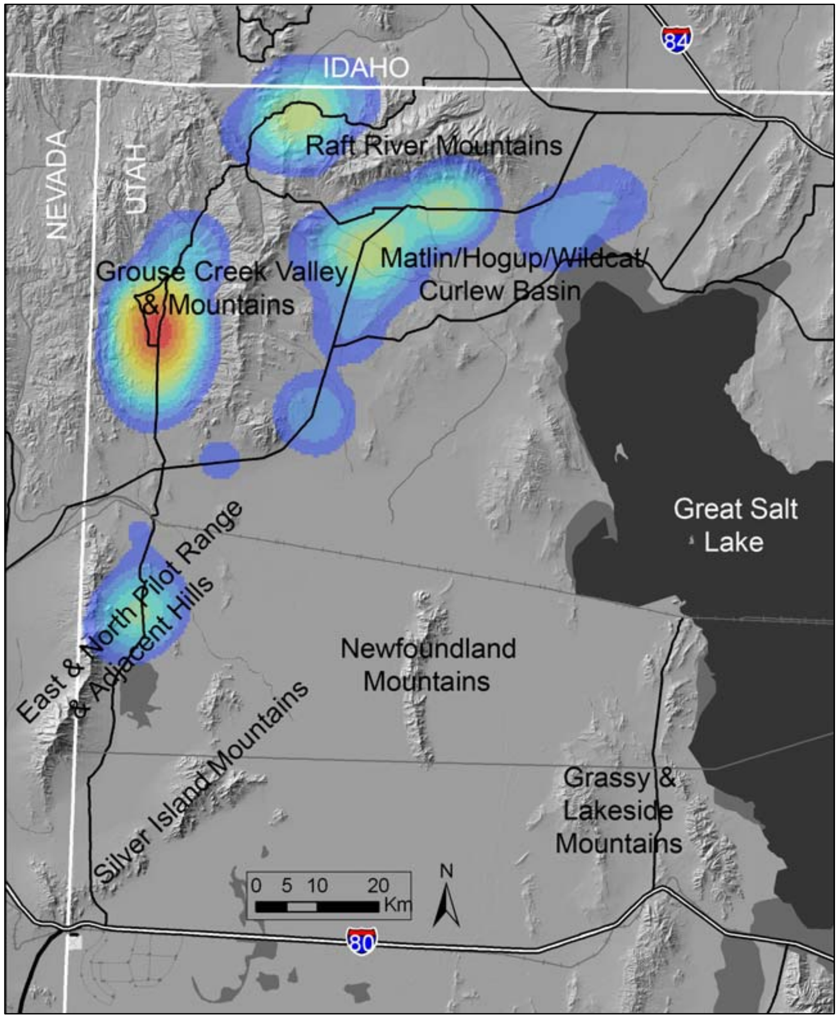

Figure C5. Density of Swainson's Hawk territories in the northwest Utah study area surveyed consecutively for ≥5 years and weighted by proportional activity (i.e., nest starts) across survey years. Darker blue areas represent lower densities of activity, while darker red areas represent higher densities.

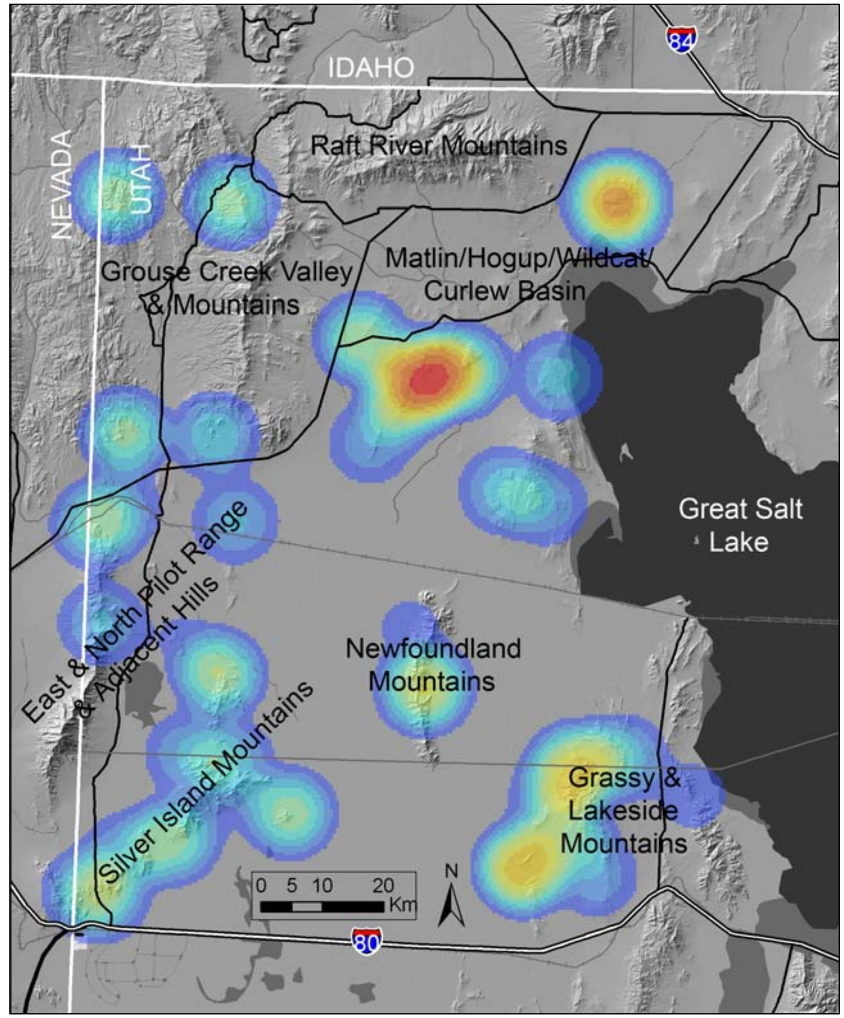

Figure C6. Density of Prairie Falcon territories in the northwest Utah study area surveyed consecutively for ≥5 years and weighted by proportional activity (i.e., nest starts) across survey years. Darker blue areas represent lower densities of activity, while darker red areas represent higher densities.

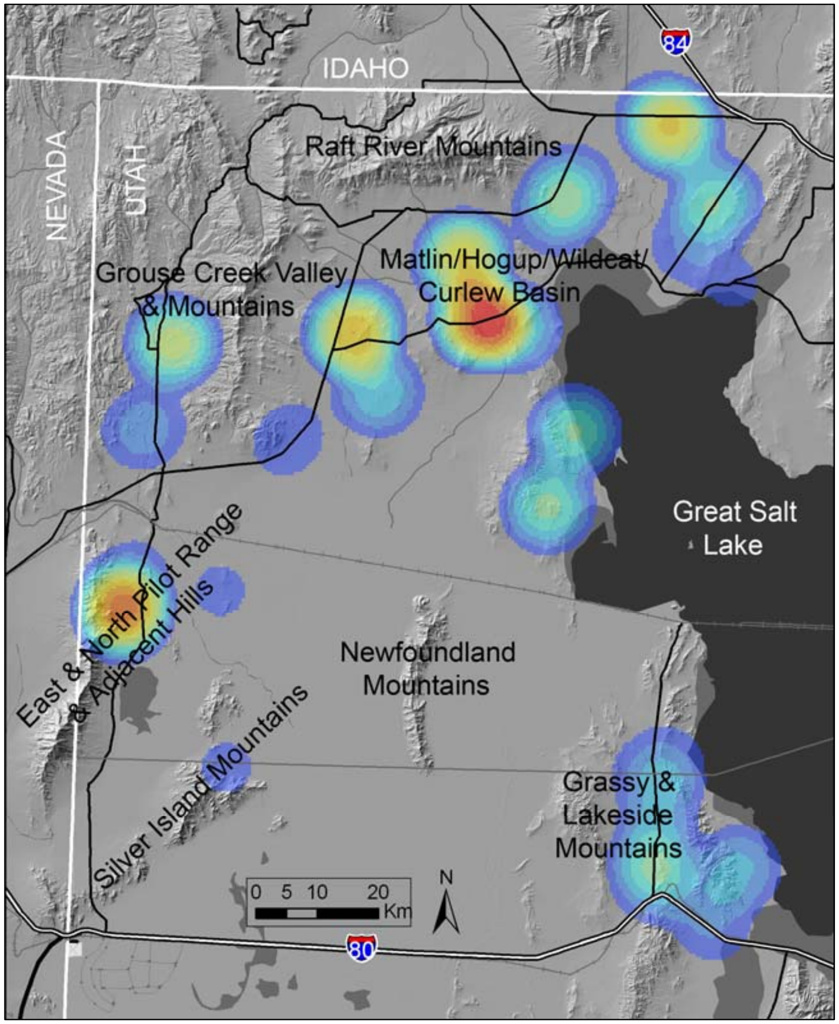

Figure C7. Density of Burrowing Owl burrows in the northwest Utah study area surveyed consecutively for ≥5 years and weighted by proportional occupancy across survey years. Darker blue areas represent lower densities of activity, while darker red areas represent higher densities.