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## RESEARCH ARTICLE

# Stable occupancy by breeding hawks (*Buteo* spp.) over 25 years on a privately managed bunchgrass prairie in northeastern Oregon, USA

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### ABSTRACT

Potential for large prairie remnants to provide habitat for grassland-obligate wildlife may be compromised by nonsustainable range-management practices. In 1979–1980, high nesting densities of 3 species of hawks in the genus *Buteo*—Ferruginous Hawk (*Buteo regalis*), Red-tailed Hawk (*B. jamaicensis*), and Swainson's Hawk (*B. swainsoni*)—were documented on the Zumwalt Prairie and surrounding agricultural areas (34,361 ha) in northeastern Oregon, USA. This area has been managed primarily as livestock summer range since it was homesteaded. Unlike in other prairie remnants, land management on the Zumwalt Prairie was consistent over the past several decades; thus, we predicted that territory occupancy of these 3 species would be stable. We also predicted that territory occupancy would be positively related to local availability of nesting structures within territories. We evaluated these hypotheses using a historical dataset, current survey and habitat data, and occupancy models. In support of our predictions, territory occupancy of all 3 species has not changed over the study period of ~25 yr, which suggests that local range-management practices are not negatively affecting these taxa. Probability of Ferruginous Hawk occupancy increased with increasing area of aspen, an important nest structure for this species in grasslands. Probability of Swainson's Hawk occupancy increased with increasing area of large shrubs, and probability of Red-tailed Hawk occupancy was weakly associated with area of conifers. In the study area, large shrubs and conifers are commonly used as nesting structures by Swainson's Hawks and Red-tailed Hawks, respectively. Availability of these woody species is changing (increases in conifers and large shrubs, and decline in aspen) throughout the west, and these changes may result in declines in Ferruginous Hawk occupancy and increases in Swainson's Hawk and Red-tailed Hawk occupancy in the future.

*Keywords:* Ferruginous Hawk, grassland birds, historical data, nesting habitat, occupancy modeling, raptor, Red-tailed Hawk, Swainson's Hawk

**Ocupación estable por 25 años de gavilanes reproductivos en un pastizal privado en el nordeste de Oregon, EEUU**

### RESUMEN

El potencial para que los grandes remanentes de praderas provean hábitat para las especies especialistas de pastizales podría verse comprometido por prácticas de manejo no sostenibles. Entre 1979 y 1980, se documentaron altas densidades de nidos de tres especies de *Buteo* (*B. regalis, B. jamaicensis, B. swainsoni*) en la pradera Zumwalt y áreas agrícolas circundantes (34,361 ha) en el nordeste de Oregon, EEUU. Esta área ha sido administrada principalmente como zona de pastoreo de ganado en el verano desde que fue convertida en un área de granjas. A diferencia de otros remanentes de praderas, el manejo de la pradera Zumwalt fue consistente a través de las décadas pasadas, por lo cual predijimos que la ocupación del territorio de estas tres especies también habría sido estable. Además predijimos que la ocupación de los territorios estaría relacionada positivamente con la disponibilidad local de las estructuras de anidación en los territorios. Evaluamos estas hipótesis usando una base de datos histórica, censos y datos de hábitat contemporáneos, y modelos de ocupación. De acuerdo con nuestras predicciones, la ocupación de los territorios de las tres especies no ha cambiado en el periodo de 25 años, lo que sugiere que las prácticas locales de manejo no tienen

un impacto negativo sobre estas especies. La probabilidad de ocupación de *B. regalis* aumentó con el incremento en el área de álamos, una estructura importante para la anidación de esta especie en los pastizales. La probabilidad de ocupación de *B. swainsoni* se incrementó con el aumento del área de arbustos grandes y la probabilidad de ocupación de *B. jamaicensis* estuvo débilmente asociada con el área de coníferas. En el área de estudio, los arbustos grandes y las coníferas son usados comúnmente como estructuras de anidación por *B. swainsoni* y *B. jamaicensis*, respectivamente. La disponibilidad de estas especies leñosas está cambiando (las coníferas y los arbustos grandes están aumentando y los álamos están disminuyendo) a través del occidente de los Estados Unidos y estos cambios podrían conducir a disminuciones de la ocupación de *B. regalis* y a aumentos en la ocupación de *B. swainsoni* y *B. jamaicensis* en el futuro.

*Palabras clave:* ave rapaz, aves de pastizal, *Buteo regalis*, *B. jamaicensis, B. swainsoni*, datos históricos, hábitat de anidación, modelos de ocupación

## INTRODUCTION

Grassland birds are threatened globally as a result of numerous factors, including habitat modification and conversion (Brennan and Kuvlesky 2005, Hoekstra et al. 2005). Most conversion of grasslands to agricultural fields occurred by the 1940s (Waisanen and Bliss 2002); thus, recent declines are attributed to other activities that alter the habitat suitability of remaining grasslands for grassland birds. These activities include modern row-crop agricultural practices that involve increased mechanization (e.g., closer row spacing) and more intensive management practices, such as extensive irrigation and increased use of pesticides (Mineau and Whiteside 2013). More intensive ranching practices such as increased stocking rates of livestock, increased fire frequency from frequent prescribed burns, and increased frequency of haying also alter grassland habitat unfavorably for grassland birds. For example, declining populations of 3 grassland passerines in the Flint Hills of Oklahoma and Kansas, the last large remnant of U.S. tallgrass prairie, may be driven by high frequency of prescribed fire and high stocking rates of livestock (With et al. 2008). Raptor use of small (2.2 ha), experimental paddocks in mesic coastal grasslands in northwestern California was higher on ungrazed areas than on grazed areas (Johnson and Horn 2008), which suggests that rangeland management practices influence raptor foraging activity. Unsustainable livestock grazing has also been hypothesized as a major factor in the decline of many raptors globally (e.g., Herremans and Herremans-Tonnoeyr 2000, Truett 2002, Ogada and Keesing 2010).

We had the unique opportunity to examine effects of livestock grazing on breeding hawks in the genus *Buteo* (hereafter "buteos") on the Zumwalt Prairie (hereafter "Zumwalt"; see below), a large grassland remnant in North America where livestock grazing has long been the predominant land use. Similar to the Flint Hills, the Zumwalt is largely privately owned and primarily managed for spring–summer livestock (mostly cattle) grazing. However, average livestock stocking rates on Zumwalt are compatible with grassland passerine conservation (Johnson et al. 2011, 2012). Fire frequencies on Zumwalt are lower now than they have been historically; low- to moderate-severity fires burned this area every 10–20 yr (Black et al. 1998, Bartuszevige et al. 2012). Currently, most fires are suppressed, unlike in the Flint Hills, where a quarter to a third of the region is burned annually.

We evaluated temporal trends in nesting territory occupancy of Ferruginous Hawk (*Buteo regalis*), Swainson's Hawk (*B. swainsoni*), and Red-tailed Hawk (*B. jamaicensis*) on Zumwalt. We resurveyed Zumwalt and reanalyzed data from surveys in 1979 and 1980, which showed high nesting densities of these species (Cottrell [now Houle] 1981). Rangewide, Ferruginous Hawks and Swainson's Hawks have declined to levels that have led to conservation concern (Collins and Reynolds 2005, U.S. Fish and Wildlife Service 2008). Declines have been attributed to habitat conversion and degradation, but persecution and secondary pesticide poisoning may play a role (Schmutz and Fyfe 1987, Bechard and Schmutz 1995, Hull et al. 2008, Schmutz et al. 2008, Bechard et al. 2010). The third species, Red-tailed Hawk, is common in North America (Preston and Beane 2009) and is known to increase in human-modified environments (Berry et al. 1998, Schmidt and Bock 2005, Stout et al. 2006). Nest-structure availability may also limit densities of buteos in prairies, as evidenced by intraspecific and interspecific agonistic interactions close to nest structures (Cottrell 1981, Janes 1987, 1994, Restani 1991). However, the utility of this literature to rangewide conservation planning is limited because none of the demographic analyses to date incorporated a probability-based random sampling approach or corrected population estimates for detection probabilities <1.0, which results in biased estimates and precludes inference beyond specific sample units (Williams et al. 2002).

Trends in territory occupancy are a good index of population performance in breeding raptors (Sergio and Newton 2003, Olson et al. 2005, Henneman et al. 2007) and other wildlife (e.g., Hossack and Corn 2007, Keane et al. 2012, Noon et al. 2012). In the present study, we used a probability-based sampling approach that allowed us to estimate variation in both site occupancy and detection rates (MacKenzie et al. 2006) and make inferences beyond our sample units to the entire Zumwalt Prairie and comparable habitats. On the basis of this body of literature

and the historical data, we developed a priori predictions about the habitat factors that might influence buteo territory occupancy, which we tested using a model selection framework.

Houle (2007) hypothesized that high densities at Zumwalt could be attributed to the management practices of the private landowners, which retained high abundances of prey and nest structures. If so, we would expect high occupancy to continue at Zumwalt, given that management practices were consistent over the 25 yr since Cottrell's study (Bartuszevige et al. 2012; for more details, see below) and because raptors have high site fidelity (Jenkins and Jackman 1993, Rosenfield and Bielefeldt 1996, Squires and Kennedy 2006).

We also predicted that nest-structure availability would influence the probability of territory occupancy, on the basis of described nesting substrates used by buteos in other sympatric populations (e.g., Schmutz et al. 1980, Bechard et al. 1990, Restani 1991, Janes 1994). We predicted that (1) area of aspen (*Populus tremuloides*) and number of rock outcrops would be positively related to Ferruginous and Red-tailed hawk territory occupancy; (2) area of conifers, mostly ponderosa pine (*Pinus ponderosa*) and Douglas-fir (*Pseudotsuga menziesii*), would be positively related to Red-tailed Hawk territory occupancy; (3) area of conifers would be negatively related to Ferruginous and Swainson's hawk territory occupancy; and (4) area of large shrubs (big enough to support a buteo nest) would be positively related to Swainson's Hawk territory occupancy.

## METHODS

### Study Area and Sample Plot Selection

Zumwalt is located in northeastern Wallowa County, Oregon, USA (117°3′N, 45°31′; Figure 1). It is the last large (~64,000 ha) remnant of Pacific Northwest bunchgrass prairie, which was formerly widely distributed (Black et al. 1998, Olson et al. 2001). The Zumwalt, unlike many prairies in the United States, is still largely intact (Kennedy et al. 2009); very little of the Zumwalt has been cultivated (~8.6% in 1938; Bartuszevige et al. 2012). It is dominated by bunchgrasses and perennial forbs. Patches of shrub and forest vegetation occur in areas with deeper soils, cooler microclimates, or higher soil moisture such as valleys, swales, slopes with northerly aspects, and riparian areas. Almost all of the Zumwalt is in private ownership. The primary land use since European-American settlement has been seasonal cattle grazing (April–October). Currently, very few people reside on the study area. Thus, human influence on the prairie is evidenced primarily by old fields and homesites that have been abandoned for more than a century (Belew 2000). In addition, there are fences and impoundments typical of open rangeland.

The original study area used in 1979–1980 was 36,361 ha (Figure 1; Cottrell 1981). In 2004, we modified the study area boundary originally defined by Cottrell (1981) to eliminate habitats that were not relatively intact native prairie. We excluded cultivated areas in the southern portion of the study area (~8,100 ha). The study area was also expanded to include additional intact grasslands (3,034 ha) not surveyed by Cottrell. Additionally, we adjusted Cottrell's northeastern and western boundaries to coincide with the prairie boundary defined by The Nature Conservancy (personal communication). Our study area (defined in 2004) was 31,136 ha (Figure 1). Landowner permission for property access was secured from 28 of 32 landowners, representing 98% of the study area.

We estimated trends in territory occupancy (presence or absence of breeding buteos at a plot; for occupancy criteria, see below) for this revised study area in 2004–2006. To estimate study area occupancy, we selected a plot size of 800 × 800 m as representative of a buteo nesting territory, on the basis of nearest-neighbor distances from Cottrell's data, and applied this plot size to the entire study area ($n = 551$ total).

We stratified the study area to reduce potential for sampling large numbers of unoccupied plots. Ninety-two percent of historical nests were found in 3 landforms: side slope, cove ravine (concave bottom of a draw), and steep slope. Using ArcGIS version 9 (ESRI, Redlands, California, USA), we combined polygons of the 3 landforms and labeled them "suitable habitat." Large areas that lacked any 1 of these 3 landforms, primarily the flat high ridgetops, were labeled "unsuitable habitat." This resulted in essentially 2 sections of suitable habitat for sampling (Figure 1). We further stratified the 2 sections of suitable habitat by historical nest densities. Using a map of historical nest locations and following natural landforms that formed boundaries (e.g., ravines and other landscape features), we drew a line between areas of high and low nest densities, thus subdividing suitable habitat into 2 areas of "high" suitability and 1 area of "low" suitability (Figure 1).

One hundred plots (18.1% of the study area) were randomly distributed in the suitable habitat, weighted by available area in the high- and low-suitability areas (Figure 1). We replaced plots on properties where we did not have access with randomly chosen accessible plots. In 2006, 2 plots were replaced because of conflicts with elk calving grounds and close proximity to a private home ("added" and "discarded" plots in Figure 1). A similar approach to stratified random sampling was used by Beck et al. (2011) to monitor Northern Goshawk (*Accipiter gentilis*) territory occupancy in the central Rocky Mountains.

### Field Data Collection

**Territory sampling.** Cottrell (1981) searched the entire area for nests; thus, we assumed that she conducted a
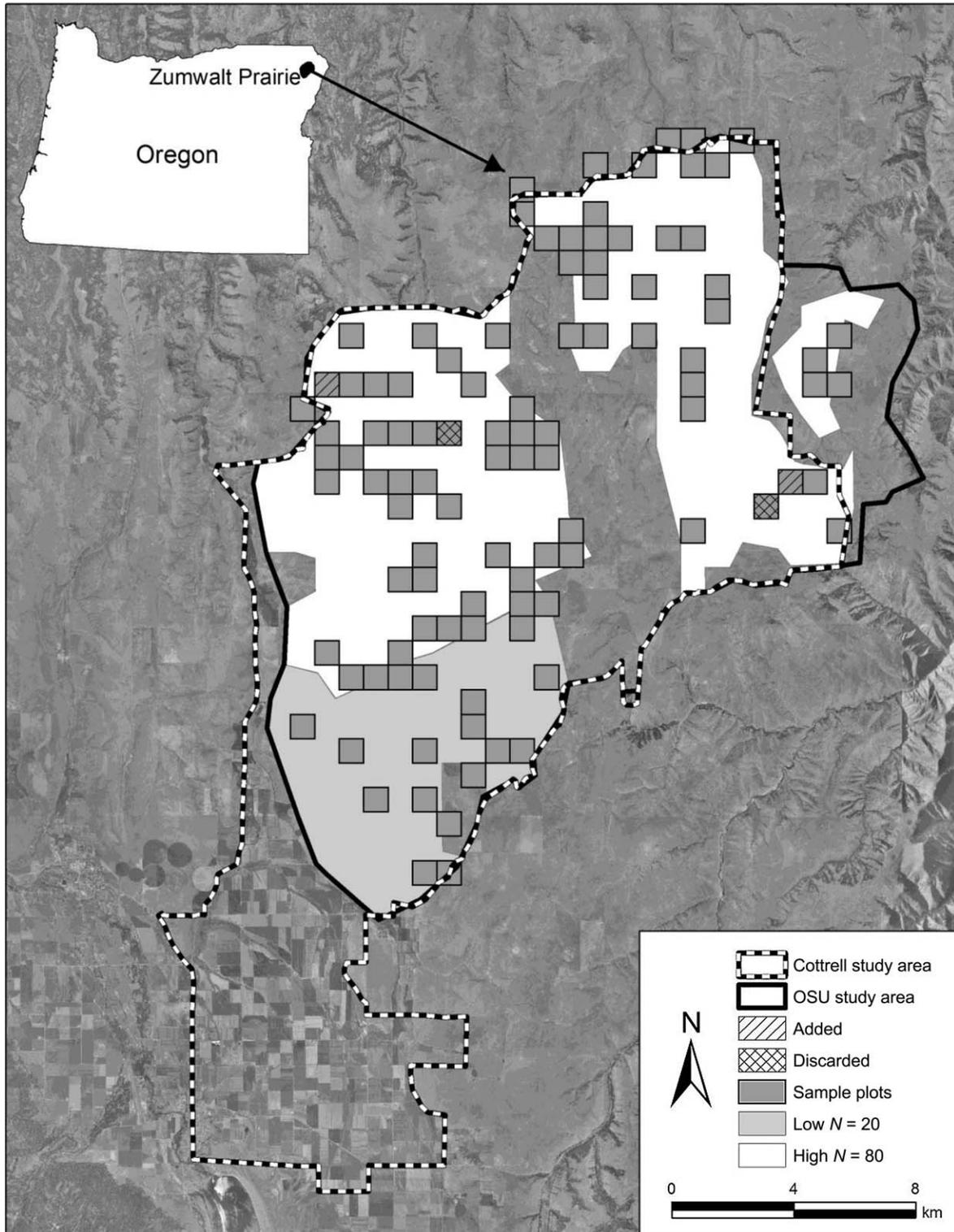
**FIGURE 1.** Location of the Zumwalt Prairie study area in northeastern Oregon, USA. The historical study area boundary (Cottrell Study Area, 1979–1980; Cottrell 1981) and current study area boundary (OSU Study Area) are depicted. Squares are plots sampled in 2004–2006. "Discarded" plots were sampled in 2004–2005, and these plots were replaced with the "added" plots in 2006. Suitable habitat was further stratified into areas of "high" (white) or "low" (medium gray) suitability on the basis of historical nest distributions. Plots surveyed in 2004–2006 were randomly distributed in these areas. For additional details, see text.

complete census of buteo nests in the study area. If Cottrell recorded nesting activity in a plot, that plot was deemed occupied; otherwise it was unoccupied. Cottrell (1981) visited plots 1–5 times; we used plots visited at least twice to estimate detection probabilities for 1979 and 1980 (see below). We sampled all plots 1–3 times $yr^{-1}$ between April 10 and July 8, 2004–2006. In 2004, we sampled each plot 2 times ($n = 187$ plot visits) using a removal design (whereby surveying halts at a plot once the species is detected; MacKenzie and Royle 2005). To improve detection probabilities, we added a third visit in 2005 ($n = 261$ plot visits). Because it is plausible for a plot to be occupied by more than 1 species, we modified the removal design as follows: If a plot was deemed occupied by 1 *Buteo* species and no other *Buteo* species were observed in the plot, that plot was not revisited. However, if another *Buteo* species was observed in that plot (but occupancy was not established for that species; see below), the plot was revisited to determine whether it was occupied by more than 1 species. This approach allowed for calculation of detection probabilities for each species, necessary for developing an occupancy model. A similar design was used by Kroll et al. (2008) to estimate occupancy of stream-associated amphibians in the Pacific Northwest.

Because they are migratory, Swainson's Hawks initiate breeding later than the other 2 species (Bechard et al. 2010). To increase the probability of detecting Swainson's Hawks (which were rarely detected during the first visit), we switched to a standard design (MacKenzie and Royle 2005) in 2006, whereby all plots were visited 3 times even if they were determined to be occupied in a previous visit ($n = 300$ plot visits).

The same 2 observers completed most plot visits (91% in 2004, 100% in 2005, and 89% in 2006); 3 other observers made the remaining visits. In all years, plots visited more than once were sampled by 2 different observers to reduce observer bias, and the sequence of observer visits was alternated when possible.

**Occupancy criteria.** During each plot visit, we searched for raptors and nest structures, noting behaviors and interactions associated with mated-pair or territorial behavior. Because many of the plots were remote and required hiking access, raptors could be recorded in a plot when the observer was not yet in that plot. For adjacent plots, a raptor observed flying between 2 plots would be recorded in both plots. Plot visits varied in length (mean = 1.5 hr; range: 0.75–8.0 hr), depending on the number of potential nest structures in the plot. Once data recording began, observers walked the entire plot, recording all nest structures and all buteos observed in the plot. A plot was deemed occupied if we observed a mated pair (based on synchronous pair flight, nonaggressive interactions with each other, or mutually aggressive behavior directed at an intruder) or a nest with eggs, nestlings, or fledglings.

**Sampling habitat covariates.** We digitized landscape features of the sample plots from 2001 digital orthophoto quadrangles using ArcGIS. We determined area of conifers, shrubs, and aspen and number of rock outcrops. We ground truthed aerial photo data between May and July 2005. "Rock outcrops" were defined as rocky features extending from the ground, >1 m tall. In 2006, we documented woody vegetation as conifer (mostly ponderosa pine and Douglas-fir); aspen; or large shrubs (i.e. big enough to support a buteo nest), mostly black hawthorn (*Crataegus douglasi*), willows (*Salix* spp.), and cotton-woods (*Populus* spp.) (hereafter "shrubs"). We also recorded the length of fences (m), which provide perches for hunting hawks, and the numbers of ponds or impoundments, which influence prey availability and livestock use.

## Statistical Analyses

**General modeling approach.** We used single-season occupancy models (MacKenzie et al. 2006) to estimate occupancy rates ($\hat{\psi}$), while also accounting for imperfect detection rates ($\hat{p}$). We used model selection procedures as described by Burnham and Anderson (2002) to rank and compare models using Akaike's Information Criterion corrected for small sample size ($AIC_c$). We considered models with $\Delta AIC_c$ values $\leq 2$ to have strong support, an appropriate criterion for a small set of single-covariate models (for a discussion of alternative $AIC_c$ criteria for multiple-covariate models, see Arnold 2010). We also evaluated Akaike weights ($w_i$) as relative measures of support for each model based on their ranking (Burnham and Anderson 2002). In addition, we used estimates of regression coefficients ($\beta$) and their 95% confidence intervals (CIs) to provide strength of evidence and support for specific effects in competitive models.

We used Program MARK version 4.3 (White and Burnham 1999) for model selection and to estimate model parameters. We present means and 95% CIs for all estimates. Lack of overlap of confidence intervals with means of other estimates was interpreted as evidence of statistical difference between estimates, whereas asymmetrical overlap of means (confidence intervals overlap one mean but not the other) was interpreted as suggestive evidence of a statistical difference between groups (Schenker and Gentleman 2001, Ramsey and Schafer 2002:674–675).

**Trend analysis.** To test our first prediction about trends in occupancy, we estimated $\hat{\psi}$ for each year (1979–1980 and 2004–2006), based only on presence of active nests (Cottrell [1981] did not record presence of mated pairs). Sparse data, lack of covariates for data collected in 1979–1980, and confounding of time and observer effects (observers were systematically assigned to surveys) resulted in very simple models incorporating time-dependent

($\hat{p}$(t)) or constant (($\hat{p}$(.)) detection rates within seasons, and a single estimate of territory occupancy across all plots for each year ($\hat{\psi}$(.)). The model structure best supported by the data was ($\hat{p}$(.)$\hat{\psi}$(.)) where parameters were estimable.

**Influence of habitat covariates on occupancy.** In the second modeling step, using data from 2006, we developed a series of a priori single-factor models based on our predictions about the 6 potential habitat factors that might influence $\hat{\psi}$ for each hawk species: amount of conifer or aspen forest (CONIFER or ASPEN; ha), amount of shrub (SHRUB; ha), number of large rocks (ROCKS) or ponds (PONDS), and linear amount of fencing (FENCE; m). We chose to develop an a priori model set that included each habitat covariate in a univariate model because, although we had a large sample of plots in all years, the number of plots where raptors were detected was quite small for many species in some years. We also chose to use only 2006 data for this analysis, because it was the largest dataset with the most surveys per plot (3 complete surveys with all occupancy criteria). For reasons similar to those previously given for the trend analysis, we did not examine the influence of covariates on $\hat{p}$. Therefore, the general model form of our models was $\hat{p}$(.)$\hat{\psi}$ (covariate).

We used the aforementioned model selection procedures to evaluate which of the 7 models (6 single habitat covariate models + the null model $\hat{p}$(.)) for each species were best supported by the data. The direction of the effect (positive or negative) of covariates included in the top models was obtained from a review of the 95% CIs of the $\hat{\beta}$ values. If the 95% CI overlapped zero, we concluded that there was weak support for an association between the covariate and $\hat{\psi}$.

## RESULTS

### Trend Analysis
Detection probabilities were <1.0 for every species and every year except for Swainson's Hawk in 1980 (Table 1). There is some support for $\hat{p}$ being higher during the historical surveys than in the current surveys for both Swainson's Hawks (asymmetrical overlap of 95% CIs for 1979 and 2006) and Ferruginous Hawks (asymmetrical overlap of 95% CIs for 1979 and 2006 and for 1980 and 2006) (Table 1). However, detection probabilities were similar for Red-tailed Hawks during all years, which suggests that differences among years may be related to the sparseness of the dataset for the 2 rarer species.

Occupancy could not be estimated for Ferruginous Hawks and Swainson's Hawks in 2004, one of the years with just 2 sampling occasions. However, all estimates of occupancy (Figure 2) support our prediction that $\hat{\psi}$ was stable over the study period. All 95% CIs of $\hat{\psi}$ for the Ferruginous Hawk and Red-tailed Hawk overlap. For Swainson's Hawk, $\hat{\psi}$ was significantly lower for 1980 than

**TABLE 1.** Estimates of detection probability ($\hat{p}$) for 3 species of *Buteo* nesting on the Zumwalt Prairie in northeastern Oregon, USA, for 1979, 1980, 2004, 2005, and 2006.

| Species | Year | $\hat{p}$ | SE | 95% CI |
|---|---|---|---|---|
| Ferruginous Hawk | 1979 | 0.82 | 0.17 | 0.34–0.98 |
| | 1980 | 0.85 | 0.14 | 0.39–0.98 |
| | 2004 | –[a] | | |
| | 2005 | 0.62 | 0.18 | 0.27–0.87 |
| | 2006 | 0.54 | 0.11 | 0.33–0.74 |
| Red-tailed Hawk | 1979 | 0.78 | 0.09 | 0.57–0.91 |
| | 1980 | 0.66 | 0.12 | 0.40–0.85 |
| | 2004 | 0.60 | 0.20 | 0.23–0.88 |
| | 2005 | 0.66 | 0.11 | 0.42–0.84 |
| | 2006 | 0.68 | 0.07 | 0.53–0.81 |
| Swainson's Hawk | 1979 | 0.66 | 0.16 | 0.33–0.89 |
| | 1980 | 1.00 | 0.00 | 1.00–1.00 |
| | 2004 | –[a] | | |
| | 2005 | 0.42 | 0.20 | 0.13–0.78 |
| | 2006 | 0.28 | 0.15 | 0.08–0.63 |

[a] Not estimated (see text).

for all other years, but this does not indicate increases in occupancy, because $\hat{\psi}$ for 1979 and 2005–2006 were similar.

The most abundant species was the Red-tailed Hawk, which occupied 12.4% (2004) to 20.7% (1979) of the Zumwalt during 1979–2006. Occupancy rates of the other 2 *Buteo* spp. were similar: Ferruginous Hawks occupied 3.8% (1979) to 11.1% (2006) and Swainson's Hawks occupied 1.1% (1980) to 11.0% (1979) of the Zumwalt during this period.

### Influence of Habitat Covariates on Territory Occupancy
Although aspen was not abundant in the study area (Table 2), model selection results (Table 3) indicated that area of aspen was positively related to Ferruginous Hawk $\hat{\psi}$ ($\beta \pm$ SE = 17.69 ± 8.84; 95% CI: 0.36–35.02; Figure 3), as predicted. There were no competing models, which contradicts our prediction that other types of nest strata influence $\hat{\psi}$ in Ferruginous Hawks. There was also no evidence that fences or ponds influenced $\hat{\psi}$ in Ferruginous Hawks.

Conifers were the most abundant woody species on the study area (Table 2). Model selection results (Table 3) indicated that area of conifers was positively related to Red-tailed Hawk $\hat{\psi}$, as predicted. However, the 95% CI of the $\hat{\beta}$ value for amount of conifer overlapped zero, indicating weak support for the effect of this covariate ($\beta \pm$ SE = 0.20 ± 0.13; 95% CI: –0.06 to 0.46; Figure 3 and Table 3). There were no competing models, which does not support our prediction that other types of nest strata influence $\hat{\psi}$ in Red-tailed Hawks. There was also no evidence that fences or ponds influenced $\hat{\psi}$ of Red-tailed Hawks (Table 3).
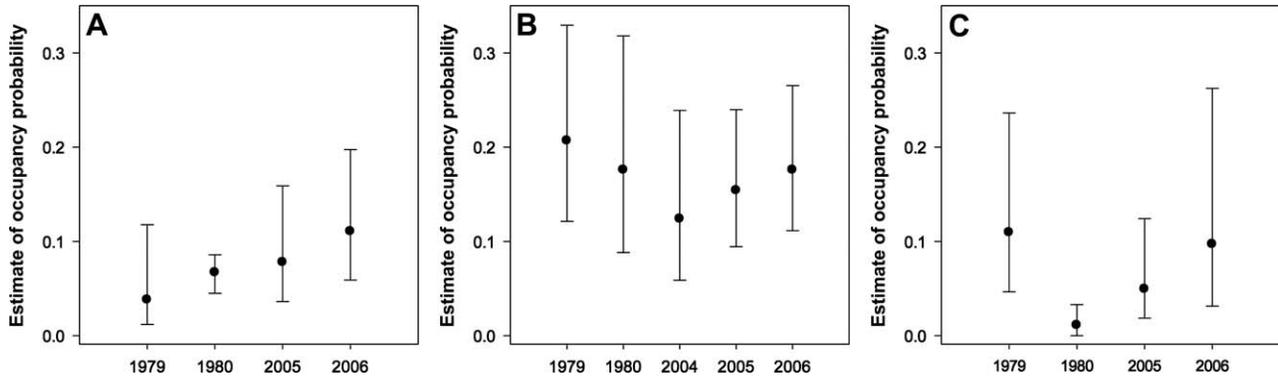
**FIGURE 2.** Year-specific occupancy estimates ($\hat{\psi}$) with 95% confidence intervals for Ferruginous Hawks (**A**), Red-tailed Hawks (**B**), and Swainson's Hawks (**C**) during the breeding season on the Zumwalt Prairie in northeastern Oregon, USA. Because of sparse data, $\hat{\psi}$ for Ferruginous and Swainson's hawks could not be estimated for 2004.

Shrubs were used by Swainson's Hawks as nest structures in the study area. Model selection results (Table 3) indicated that area of shrubs was positively associated with Swainson's Hawk $\hat{\psi}$, as predicted ($\beta \pm SE = 1.07 \pm 0.41$; 95% CI: 0.27–1.87; Figure 3). There were no competing models, which does not support our prediction that other types of nest strata influence $\hat{\psi}$ in Swainson's Hawks (Table 3).

## DISCUSSION

Combining a historical dataset with more recent surveys that incorporated stratified random sampling allowed us the unique opportunity to assess patterns in territory occupancy of Ferruginous, Red-tailed, and Swainson's hawks on one of the last large bunchgrass prairie remnants in North America. Our results support the results of other investigations (e.g., Johnson et al. 2011, 2012) that grassland birds of conservation concern do not necessarily decline over time in working landscapes in the western United States. Zumwalt is providing habitat for the Ferruginous Hawk and Swainson's Hawk, species that are declining in other parts of their ranges (Collins and Reynolds 2005, U.S. Fish and Wildlife Service 2008). The ability of this working landscape to support these species is likely due to the fact that Zumwalt has not been extensively modified by the anthropogenic activities that typically threaten grasslands (e.g., conversion to cropland, fragmentation from exurban development, and increasing extent and frequency of fire; Bartuszevige et al. 2012). In addition, there is no evidence that the Red-tailed Hawk is expanding its occupancy in the study area, which commonly occurs as a result of anthropogenic change in other areas (e.g., Berry et al. 1998, Schmidt and Bock 2005, Stout et al. 2006). However, our occupancy estimates for this species have large confidence intervals, so it is possible that our analysis did not detect increases or decreases that

may have occurred in the past 25 yr. In addition, our study provides only "snapshots" in time; without a more complete time series, we have no understanding of the range of variation in occupancy rates that characterize raptors on the Zumwalt prairie over time. That said, this is one of the few studies to estimate raptor territory occupancy rates while taking into account detection rates <1.0 and providing estimates of sampling variance. The few studies that have estimated detection of breeding buteos are not directly comparable because they used different survey techniques. Henneman et al. (2007) estimated that detection of Red-shouldered Hawks (*B. lineatus*) from call-broadcast surveys in central Minnesota ranged from 0.28 to 0.54. Using aerial surveys, Ayers and Anderson (1999) and Booms et al. (2010) estimated that detection ranged from 0.24 to 0.37 for Ferruginous Hawks nesting in south-central Wyoming and from 0.10 to 0.42 for cliff-nesting Rough-legged Hawks (*B. lagopus*) in western Alaska, respectively.

Although agricultural management practices on Zumwalt have not changed during the past ~30 yr, landscape changes have occurred as a result of these practices. The most dramatic change in this landscape is the shift in the abundance of woody species, the primary nesting substrates for the 3 species of *Buteo* in this area (84.5% of all

**TABLE 2.** Values of habitat covariates collected in occupancy plots (see Figure 1 for plot locations) during 2005 in the Zumwalt Prairie in northeastern Oregon, USA.

| Habitat covariate | Mean ± SE | Range |
|---|---|---|
| Aspen (ha) | 0.06 ± 0.02 | 0.00–2.17 |
| Conifers (ha) | 0.59 ± 0.27 | 0.00–22.07 |
| Shrubs (ha) | 0.37 ± 0.08 | 0.00–4.34 |
| Large rocks (*n*) | 4.25 ± 0.53 | 0.00–21.00 |
| Ponds (*n*) | 1.07 ± 0.08 | 0.00–3.00 |
| Fence (m) | 1.30 ± 0.09 | 0.00–4.34 |

**TABLE 3.** Model selection results for all models with $\Delta AIC_c < 4$. These models estimate the effect of a priori habitat variables on occupancy ($\hat{\psi}$) of Ferruginous, Red-tailed, and Swainson's hawks nesting on the Zumwalt Prairie in northeastern Oregon, USA, during 2006. Model covariates include acreage of coniferous or aspen forest (CONIFER or ASPEN; ha), acreage of large shrubs (SHRUB; ha), number of large rocks (ROCKS), and linear amount of fencing (FENCE; m) in each plot. Model weights ($w_i$), model deviance, and number of parameters ($k$) are also given for all models. "Sign" refers to the regression coefficient corresponding to the habitat variable: positive (+) or negative (–) if 95% confidence intervals for the coefficient do not overlap zero, and zero otherwise.

| Models | $AIC_c$ | $\Delta AIC_c$ | $w_i$ | $k$ | Deviance | Sign |
|---|---|---|---|---|---|---|
| Ferruginous Hawk | | | | | | |
| $\hat{p}(.)\hat{\psi}(ASPEN)$ | 179.82 | 0.00 | 0.82 | 3 | 173.57 | + |
| Red-tailed Hawk | | | | | | |
| $\hat{p}(.)\hat{\psi}(CONIFER)$ | 239.48 | 0.00 | 0.50 | 2 | 237.56 | 0 |
| $\hat{p}(.)\hat{\psi}(.)$ | 241.69 | 2.21 | 0.17 | 3 | 233.23 | NA |
| $\hat{p}(.)\hat{\psi}(FENCE)$ | 243.23 | 3.75 | 0.08 | 3 | 236.98 | 0 |
| $\hat{p}(.)\hat{\psi}(ROCK)$ | 243.45 | 3.97 | 0.07 | 3 | 237.20 | 0 |
| Swainson's Hawk | | | | | | |
| $\hat{p}(.)\hat{\psi}(SHRUB)$ | 100.24 | 0.00 | 0.77 | 3 | 93.99 | + |

known nest structures, $n = 84$; P. L. Kennedy et al. personal observation). Aspen has declined by 18% (from 7.2 ha in 1976 to 5.9 ha in 2005) in Zumwalt, and there is little or no regeneration of the current decadent clones. Ponderosa pine and shrubs have increased by 455% (from 10.8 ha in 1976 to 60.0 ha in 2005) and 72% (from 21.8 ha in 1976 to 37.5 ha in 2005), respectively. This declining trend in aspen is common throughout the western United States. Multiple land-use factors (e.g., fire suppression and livestock herbivory) and ecological factors (e.g., native ungulate herbivory and climate change) influence these trends (Brookshire et al. 2002, Frey et al. 2004, Rehfeldt et al. 2009).

In our study area, decline in aspen can partially be attributed to high levels of native and domestic ungulate grazing and differences in the palatability of the woody species (Bartuszevige et al. 2012). The invading species, conifers and hawthorns, are less palatable to ungulates (Kauffman and Krueger 1984, Darambazar et al. 2013), whereas aspen is a particularly desired foraging substrate for elk (Wooley et al. 2008) and is also eaten by cattle. Therefore, there are few unprotected aspen stands where new stems are able to grow tall enough to escape increased pressure from browsing due to high abundance of ungulates (see two unpublished reports by R. V. Taylor and coauthors: http://bit.ly/1bplH41, http://bit.ly/1gglzGt). Herbivory by domestic and native ungulates is a well-documented chronic disturbance that can affect vegetation dynamics globally (e.g., Wisdom et al. 2006, Albon et al. 2007, Endress et al. 2012). Given that aspen is a strong predictor of Ferruginous Hawk occupancy, it is possible that continued decreases in the availability of this nest structure will result in future declines of this species on Zumwalt unless they switch to other nest structures, which they have used on the study area (e.g., ponderosa pine and rock outcrops) and are known to use in other parts of their range (Bechard and Schmutz 1995). Conversely, increases in shrub and pine could result in higher occupancy of Swainson's Hawks and Red-tailed Hawks, respectively.

The Red-tailed Hawk has replaced the forest-dwelling Red-shouldered Hawk in partially cleared hardwood bottomland forests in the eastern United States. It has also become more common through the northern Great Plains during the past 100 yr, likely as a result of increased tree growth in formerly treeless grasslands (Preston and Beane 2009). Thus, if tree encroachment continues in this grassland, we predict that Red-tailed Hawks will replace Ferruginous and Swainson's hawks in Zumwalt in the future.

In addition to the availability of nest structures, prey availability and interspecific competition for nest sites may also influence territory occupancy (Squires and Kennedy 2006, Tapia et al. 2007, Dugger et al. 2011). The fact that different nest structures were associated with the occupancy rates of each species suggests that these 3 species may partition resources to avoid competition for a limited resource (Restani 1991, Carrete et al. 2005). However, we did not test any hypotheses related to these factors in the present study. Future studies on this topic should examine the influence of prey and congeners on occupancy.

### Study Limitations

Combining historical data collected using traditional techniques with a dataset collected using current survey methods allowed us to use modern analytical approaches (for a similar approach, see Kotliar et al. 2007). This enabled us to assess trends in model parameters based on datasets collected 25 yr apart. Caution must be exercised when using historical data, however. We were forced to make assumptions about the original sampling regime (e.g., a census of the entire study area) to fit the current analysis, which may have influenced parameter estimates for 1979–1980. Also, our stratified random sample of the prairie included many areas that were not sampled in the original study (Figure 1). This resulted in a large number of
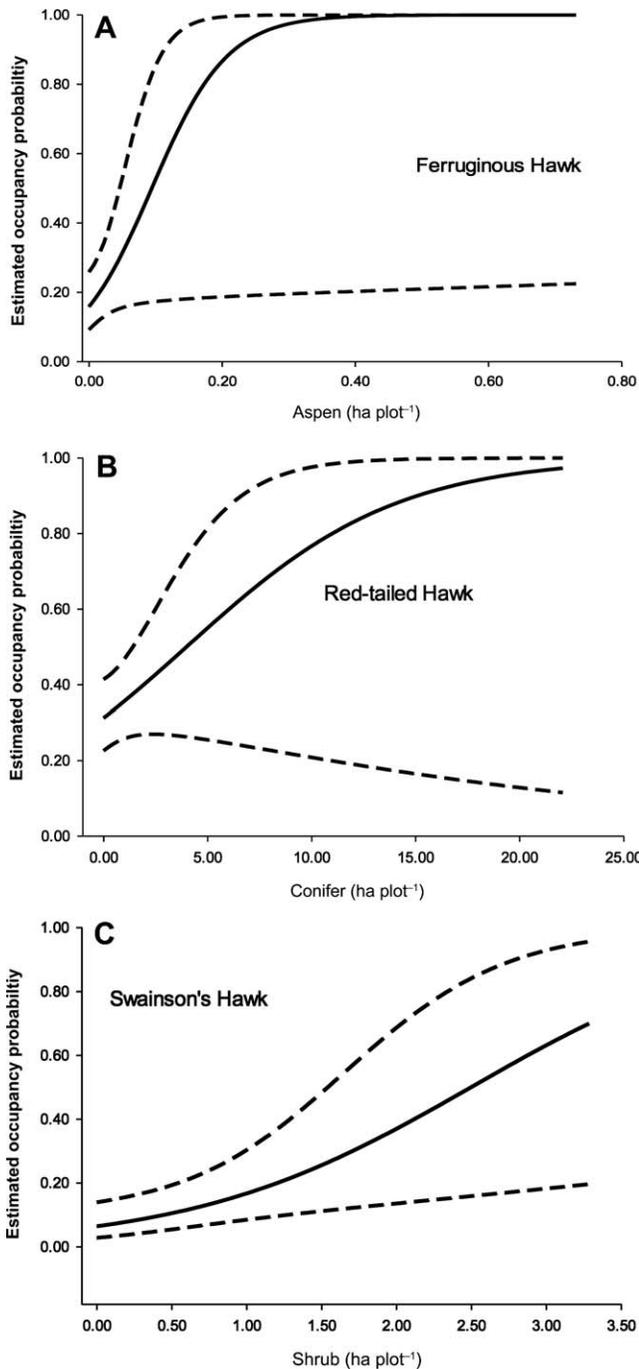
**FIGURE 3.** Predicted estimates of occupancy ($\hat{\psi}$) with 95% confidence intervals from our top models for Ferruginous Hawks, Red-tailed Hawks, and Swainson' Hawks during the breeding season on the Zumwalt Prairie in northeastern Oregon, USA (see Table 3 for top models). These were based on the 2006 data and were plotted across the range of covariate values observed in our 800 x 800 m plots.

zeros in our dataset, which influenced our ability to model all parameters and covariates simultaneously or with much structure. It also eliminated the possibility of using multiseason occupancy models (MacKenzie et al. 2006)

to evaluate effects of temporal changes in territory turnover. We might have been able to reduce the number of zeros by incorporating an additional stratification factor: whether an area had been searched previously. However, this additional stratificaion would also have reduced our ability to infer results for the entire prairie. The data sparseness was particularly problematic in 2004, when we had only 2 sampling occasions. In that year, we could not estimate $\hat{\psi}$ accurately for the 2 rare species. Thus, future studies of territory occupancy for these species should incorporate a minimum of 3 sampling occasions and/or increase the number of plots sampled.

Finally, our results support the findings of other raptor studies (e.g., Henneman et al. 2007, Booms et al. 2010) that breeding raptors are not 100% detectable. In the present study, Swainson's Hawks had the lowest detection probabilities, which are likely a result of their small sample sizes, late arrival on the study area, smaller nest size, nest placement (commonly embedded in dense hawthorn shrubbery), and secretive, nondefensive behavior toward nest-site intruders. The detection rate of 1.0 for Swainson's Hawks during 1980 is likely inflated as a result of superimposing detection probabilities on a small set of initial observations that were collected using a different methodology.

## ACKNOWLEDGMENTS

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