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RESEARCH ARTICLE

## How effective is the Safe Harbor program for the conservation of Red-cockaded Woodpeckers?

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### ABSTRACT

Land use restrictions imposed by the Endangered Species Act may create conflict, affecting conservation on private lands. In 1995, the Safe Harbor program (hereafter, 'Safe Harbor') was initiated to alleviate concerns of private landowners about conservation of imperiled species. The inaugural program targeted endangered Red-cockaded Woodpeckers (*Picoides borealis*; hereafter, 'RCW') in the North Carolina Sandhills, USA. Landowners enrolled in the Safe Harbor select management actions to enhance habitat for existing populations, but incur no additional responsibilities for increases in populations. Despite the relevance for conservation, the benefits of Safe Harbor remain largely unknown. Here, we evaluate the effects of Safe Harbor on RCWs in the North Carolina Sandhills. Between 1980 and 2014, we monitored 55 RCW territories (30 Safe Harbor, 25 control). Following the initiation of Safe Harbor, the probability of territory abandonment on control properties increased by ~14% over a 19-yr period, while it remained constant on Safe Harbor properties. This could have been due to more Safe Harbor properties (87%) than control properties (68%) receiving artificial cavities that offset cavity losses. Following the initiation of Safe Harbor, the laying date on Safe Harbor properties advanced 16.1 days over a 19-yr period, compared with 11.6 days on control properties. Enrollment in Safe Harbor was not related to other measures of breeding performance, likely due to variation in habitat management across properties. While Safe Harbor clearly alleviates conflict over conservation, other effects depend on management actions. We encourage evaluations of existing similar programs to determine their efficacy.

**Keywords:** breeding biology, Endangered Species Act, habitat management, incentive program, *Picoides borealis*, reproduction

### ¿Qué tan efectivo es el Programa Puerto Seguro para la conservación de *Picoides borealis*?

### RESUMEN

Las restricciones al uso de la tierra impuestas por la Ley de Especies en Peligro de Extinción pueden generar conflictos, afectando la conservación en tierras privadas. En 1995, se inició el Programa Puerto Seguro para disminuir la preocupación de los propietarios de tierras privadas sobre la conservación de especies en peligro. El programa inaugural se enfocó en la especie en peligro *Picoides borealis*, en las colinas de arena de Carolina del Norte. Los propietarios de la tierra se enrolaron en determinadas acciones de manejo en el marco de Puerto Seguro para mejorar el hábitat para las poblaciones existentes, pero no se vieron comprometidos con responsabilidades adicionales a partir del incremento de la población. A pesar de la relevancia para la conservación, los beneficios de Puerto Seguro siguen siendo mayormente desconocidos. Aquí, evaluamos los efectos de Puerto Seguro sobre *P. borealis* en las colinas de arena de Carolina del Norte. Entre 1980 y 2014, monitoreamos 55 territorios de *P. borealis* (30 Puerto Seguro, 25 control). Luego del inicio de Puerto Seguro, la probabilidad de abandono del territorio en las propiedades control aumentó un ~14% sobre un período de 19 años, mientras que permaneció constante en las propiedades de Puerto Seguro. Esto podría deberse a que más propiedades de Puerto Seguro (87%) recibieron cavidades artificiales en comparación con las propiedades control (68%), compensando las pérdidas de cavidades. Luego del inicio de Puerto Seguro, la fecha de puesta en las propiedades de Puerto Seguro avanzó 16.1 días sobre un período de 19 años, comparado con 11.6 días en las propiedades control. El enrolamiento en Puerto Seguro no se relacionó con otras medidas de desempeño reproductivo, probablemente debido a la variación en el manejo del hábitat entre las propiedades. Mientras que Puerto Seguro claramente alivia el conflicto por la conservación, otros impactos dependen de la acción de manejo. Alentamos las evaluaciones de los programas similares existentes para determinar su eficacia.

*Palabras clave:* biología reproductiva, Ley de Especies en Peligro de Extinción, manejo del hábitat, *Picooides borealis*, programa incentivo, reproducción

## INTRODUCTION

The Endangered Species Act (ESA) was enacted in 1973 to conserve endangered and threatened species across the United States. Under section 9 of the ESA, 'take' of listed species is prohibited, unless authorized under other ESA provisions. Take includes harm, defined as an act that kills or injures listed wildlife by significantly impairing essential behavioral patterns, and extends to significant habitat modification. Therefore, the ESA imposes land use restrictions that may have economic consequences for landowners, who may consequently be reluctant to engage in active habitat management for endangered and threatened species. This reluctance may be particularly evident on private lands, where landowners are not legally obligated under the ESA to participate in habitat management for listed species, even though they must avoid land uses and habitat modifications that could harm listed wildlife residing on their properties. In contrast, under section 7 of the ESA, managers of public lands are required to conserve species through beneficial management actions that sustain and increase target populations. In response to the restrictions imposed by the ESA, private landowners may actively remove unoccupied habitat to discourage listed species from settling on their land. Because the vast majority of species listed under the ESA occur on private land (USGAO 1994), the responses of private landowners to the restrictions imposed by the ESA potentially have substantial consequences for the conservation of imperiled species that require active management to maintain and increase their habitats and populations.

The Safe Harbor program (hereafter, 'Safe Harbor') was initiated by the U.S. Fish and Wildlife Service in 1995 to address conflicts over conservation on private lands (Bonnie 1997). Landowners enrolled in this nationally recognized voluntary program are obligated to undertake conservation measures (i.e. habitat management) that benefit existing (baseline) populations of target species on their land, but are allowed 'incidental take' for any expansion of the population beyond baseline levels. Thus, Safe Harbor eases the regulatory burden and removes uncertainties associated with future land management, thereby facilitating conservation and reducing fear of increased land use restrictions. Between its inception in 1995 and 2002, >8,000 km<sup>2</sup> was enrolled in Safe Harbor, providing protection for more than 21 endangered species in the U.S. through targeted habitat management (Wilcove and Lee 2004). Yet, despite the program's focus on conservation, little is known about the effects of Safe Harbor on target species.

The inaugural Safe Harbor program targeted Red-cockaded Woodpeckers (*Picooides borealis*; hereafter, 'RCWs') in the North Carolina Sandhills. The RCW is a cooperatively breeding species that typically inhabits mature pine forests in the southeastern U.S. (Walters and Garcia 2016). RCWs are primary cavity nesters that excavate cavities exclusively in live mature pine trees. Within a family group, each bird has a cavity in which it roosts. Collectively, all cavities used by the family constitute a cluster. RCWs prefer open, fire-maintained forest with a sparse hardwood midstory and species-rich grass and forb ground cover for breeding and foraging (USFWS 2003). Because of loss and degradation of habitat, RCWs experienced a dramatic population decline, leading to their listing as Federally Endangered under the ESA in 1970. Now, they generally require active habitat management (e.g., prescribed fire and silviculture) to regulate forest structure and composition. Although they are recovering, numbers remain at <3% of the estimated original population (Conner et al. 2001). Longleaf pine (*Pinus palustris*) forests in the North Carolina Sandhills support one of the largest remaining populations of RCWs. While state and federal lands provide much of the existing habitat for RCWs in the area, ~10% of the population occurs on private lands. Negative attitudes of landowners toward conservation of RCWs resulted in loss of habitat in the early 1990s—Landowners removed pine habitat to avoid colonization of their properties by RCWs and resultant land use restrictions (Lueck and Michael 2003). These negative attitudes and landowner actions raised concerns about the long-term viability of RCWs on private lands and led to the inception of Safe Harbor in 1995 (Bonnie 1997).

Over the 2 decades that the Sandhills Safe Harbor program has been in place, management of RCW foraging habitat on Safe Harbor properties has been variable. This is partly due to the nature of the Sandhills program: Landowners who enroll in Safe Harbor are able to select among beneficial management strategies when drafting the agreement. Thus, the habitat management techniques used across Safe Harbor properties are not consistent. Nevertheless, the primary management activity conducted on Safe Harbor properties has been construction of artificial cavities. Cavities can be added to active clusters with few existing cavities (cavity-limited clusters) to reduce the probability of cluster abandonment, or constructed in unoccupied habitat (recruitment clusters) to promote population expansion (Copeyon et al. 1991, Walters 1991). Restrictor plates have also been affixed to enlarged cavities to prevent cavity abandonment and to discourage

larger heterospecific occupants (Carter et al. 1989). In addition, landowners are often required to maintain or enhance existing foraging habitat following standards based on total basal area ( $\geq 280 \text{ m}^2$ ) of pines  $\geq 30$  yr of age and  $\geq 25$  cm dbh in open ( $9\text{--}16 \text{ m}^2 \text{ ha}^{-1}$ ) stands with little hardwood midstory (USFWS 2003). The main aims of these management activities have been to avoid the destruction of RCW-occupied habitat and to maintain existing RCW habitat in order to connect otherwise isolated subpopulations.

Results to date suggest that Safe Harbor has enhanced RCW population connectivity in the Sandhills (Trainor et al. 2013). However, the effects of Safe Harbor on other aspects of RCW biology remain unknown. The quality and quantity of available foraging habitat affect the productivity of RCWs (Davenport et al. 2000, McKellar et al. 2014, Garabedian et al. 2017). However, foraging habitat management standards prescribed for Safe Harbor are not associated with RCW breeding performance (Walters et al. 2002). Nevertheless, habitat management activities on Safe Harbor properties may improve habitat over that on adjacent unmanaged properties. If so, RCWs breeding on Safe Harbor properties should experience enhanced breeding performance compared with those on adjacent unmanaged properties. The RCW Safe Harbor program in the Sandhills was the first Safe Harbor program to be established, offering the longest period of implementation over which to evaluate the effects of a program with its structure.

Our objective was to evaluate the effects of Safe Harbor on RCWs by comparing the biology of birds breeding on Safe Harbor properties with those breeding on adjacent control properties using a Before-After-Control-Impact study design. We predicted that birds breeding on Safe Harbor properties would experience enhanced breeding performance compared with those breeding on control properties. Specifically, we predicted that birds breeding on Safe Harbor properties would: (1) lay larger clutches; (2) experience less nest failure; (3) experience less brood reduction; and (4) experience higher productivity. In addition, because food availability can limit egg laying (Perrins 1970), and because food availability is often associated with habitat quality (Johnson 2007), we predicted that birds breeding on Safe Harbor properties would initiate clutches earlier than their counterparts breeding on control properties. Because of the addition of artificial cavities on Safe Harbor properties, we also predicted that the number of abandoned clusters would be lower on Safe Harbor properties compared with adjacent control properties. Finally, we explored 2 additional aspects of demography that may be influenced by habitat quality, adult female survival and the probability of emigration by adult females.

## METHODS

### Study Area

We conducted our study on private lands in Hoke and Moore counties in the North Carolina Sandhills (centered on  $35.1667^\circ\text{N}$ ,  $79.4500^\circ\text{W}$ ; Figure 1). The study area covered  $\sim 260,000$  ha and contained a population of RCWs that had been monitored annually since the early 1980s. Between 1995 and 2014,  $\sim 22,000$  ha of land within the study area was enrolled into Safe Harbor. Much of the habitat consisted of an open canopy dominated by mature longleaf pine, with a sparse midstory composed primarily of oaks (*Quercus* spp.) and ground cover dominated by pineland threeawn (*Aristida stricta*). The study area also included golf courses, horse farms with wooded pastures, and residential developments that supported a large proportion of RCW clusters found on Safe Harbor properties.

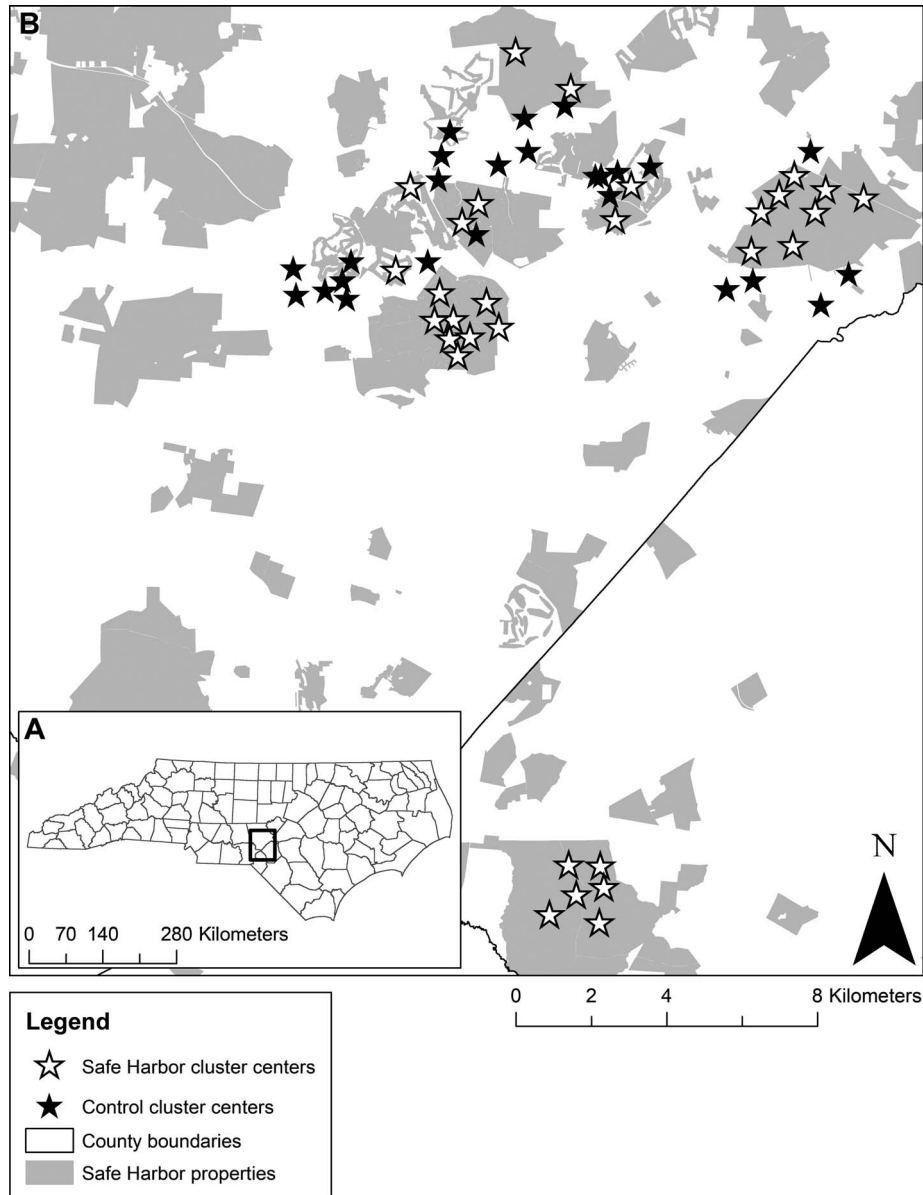
### Experimental Approach

We used a Before-After-Control-Impact (hereafter, 'BACI') study design to evaluate the effects of Safe Harbor on RCWs. Specifically, we compared pre- and post-enrollment measures of breeding performance of birds on properties enrolled in Safe Harbor (i.e. those affected) with those on control properties between 1980 and 2014. The BACI design is a common approach used in impact assessments (e.g., Stephens et al. 2015, Winder et al. 2015, Sansom et al. 2016) and allows researchers to separate the effects of an impact on target variables from natural variability in those variables.

### Breeding Performance

Monitoring methods are described in detail by Walters et al. (1988). In brief, we visited all clusters in the study area prior to each breeding season to determine whether the cluster was occupied (indicated by the presence of at least one adult). Thereafter, we monitored the contents of cavities within each active cluster (e.g., clutch and brood size) every 9–11 days. We also identified color-banded adults to obtain group size and composition. At 5–10 days posthatching, we banded nestlings with a unique combination of color bands. We conducted fledgling checks at 30 days posthatching to determine the identity and sex of fledged young.

We defined group size as the number of adults in a breeding group (2 breeding adults plus 0–5 helpers; Walters and Garcia 2016). We considered the initiation of a clutch to indicate the onset of a breeding attempt (hereafter, 'laying date'). We calculated laying date by backdating from the estimated age of nestlings when first observed, assuming that 1 egg was laid per day and that the interval between clutch completion and hatching was 11 days (Schiegg et al. 2002). We considered a breeding



**FIGURE 1.** Location of the study area within (A) North Carolina, USA, and (B) Hoke and Moore counties, North Carolina, where we evaluated the effectiveness of the Safe Harbor program for the conservation of Red-cockaded Woodpeckers.

attempt to have failed if no young fledged (hereafter, 'breeding failure'). We calculated brood reduction as the difference between the clutch size and the number of nestlings banded as a proportion of clutch size (most brood reduction occurs in the first couple of days posthatching; LaBranche and Walters 1994). Finally, we defined productivity as the number of fledglings produced annually per group.

#### Landscape Attributes

We mapped all cavity trees and calculated the centroid for each cluster as the mean of the cavity tree coordinates

within the cluster using ArcMap 10.3 (Environmental Systems Research Institute, Redlands, California, USA). For the purpose of analysis, we used the same cluster centroid throughout the entire study because cavity trees are typically used for long periods (i.e. up to and exceeding 30 yr; Conner et al. 2001). We delineated territories by centering circular buffers with a 0.5-km radius on each cluster centroid following Walters et al. (1988). Our buffers approximated the size of an average core area within an RCW territory in the study area (i.e. the area in which an RCW group spent 95% of its time [81 ha]; Conner et al. 2001). We used Thiessen polygons to partition neighboring



territories when buffers overlapped (Convery and Walters 2004). We mapped Safe Harbor properties and then calculated the percentage of each territory located within a Safe Harbor property (hereafter, 'percentage Safe Harbor'). We considered territories with cluster centroids within a Safe Harbor property as experimental (i.e. enrolled in Safe Harbor), and territories with cluster centroids outside Safe Harbor properties as untreated control clusters (i.e. not enrolled in Safe Harbor). We assigned each control cluster an enrollment year equivalent to the enrollment year of its nearest Safe Harbor cluster.

### Statistical Analysis

**Breeding performance.** We developed a set of a priori mixed models in PROC GLIMMIX in SAS (SAS Institute 1990) to evaluate the effects of Safe Harbor on the breeding performance of RCWs. Because measures of breeding performance can change between breeding attempts (LaBranche and Walters 1994, Conner et al. 2001), we considered only first breeding attempts in each year, except for the productivity analysis, for which we considered all breeding attempts. In the productivity analysis, we also considered potential breeding attempts (i.e. where the presence of a breeding pair made breeding possible, but where no breeding attempt was initiated). Laying date (day 1 = April 2) was square root transformed to meet normality assumptions. We fitted models evaluating clutch size and productivity with Poisson error distributions and log link functions. Cluster abandonment and breeding failure were analyzed as binary outcomes (e.g., yes–no or success–failure) and modeled using binomial error distributions and logit links. Brood reduction was modeled using a binomial error distribution and events–trials syntax, and models were fitted with logit links. In all models, we included treatment as a categorical dummy variable (Safe Harbor = 1, control = 0), years since enrollment as a continuous variable (data collected before enrollment were assigned a value of 0), and an interaction between treatment and years since enrollment. We considered cluster ID as a random factor to account for repeated measures within each cluster, and year as a categorical fixed effect to account for annual variation in breeding performance. We included the percentage of territory enrolled in Safe Harbor ('percentage Safe Harbor') to account for potential effects of differences in Safe Harbor coverage among clusters. Given that time since enrollment and percentage Safe Harbor were inherently correlated (i.e. percentage Safe Harbor was always greater after enrollment), we kept percentage Safe Harbor constant and equal to the percentage at enrollment for each cluster throughout the analysis, and included an interaction between years since enrollment and percentage Safe Harbor to avoid multicollinearity. Finally, to control

for other factors known to affect breeding performance, we included group size (Walters and Garcia 2016), laying date (LaBranche and Walters 1994, Conner et al. 2001), and age of male and female breeders (Conner et al. 2001) as covariates. We evaluated collinearity between explanatory variables by calculating Spearman's rank correlation coefficients ( $r_s$ ), and constructed models using combinations of explanatory variables that were not correlated ( $r_s < 0.5$ ) to reduce the probability of making Type II errors (Dormann et al. 2013).

We estimated model parameters using the maximum likelihood technique with Laplace approximation (Bolker et al. 2009). We assessed the goodness-of-fit of each global model using Pearson's  $\chi^2/df$ . We performed a multistep, step-down model selection process by first testing for an effect of year on measures of breeding performance independently from other explanatory variables and pooling data when year had no effect. We then constructed candidate models by incorporating explanatory variables. We used Akaike's information criterion corrected for small sample size ( $AIC_c$ ), differences in  $AIC_c$  ( $\Delta AIC_c$ ), and model weights ( $w_i$ ) to assess models in our candidate sets. We considered the model with the lowest  $AIC_c$  to be the top-ranked model, and models with  $\Delta AIC_c \leq 2$  to have substantial support from the data (Burnham and Anderson 2002), unless they included the addition of an uninformative parameter (Arnold 2010). We considered a parameter uninformative if its addition to a less complex competing model resulted in  $\Delta AIC_c \leq 2$ , and thus did not explain enough variation in the data to warrant its inclusion. We present parameter estimates as means with 95% confidence intervals. We considered parameter estimates significant if their 95% confidence intervals did not include zero.

**Survival and emigration.** We constructed 2-way contingency tables and used chi-square tests of independence to evaluate whether adult female survival and emigration were independent of treatment. Treatment levels were (1) Safe Harbor and (2) control properties before enrollment, and (3) Safe Harbor and (4) control properties after enrollment. Survival events were classified into 2 categories: survived or died in a given year. We considered a bird to have died during a given year if it was not observed in the following year. Emigration events were classified into 2 categories: left a cluster (i.e. emigrated), or remained in the same cluster between 2 consecutive years (i.e. did not emigrate). We were able to distinguish between emigration and survival events because the detection probability of birds in our study population is very nearly one, as only a small number of birds disperse out of the wider study area annually (Walters et al. 1988). Of those that disperse out of the wider study area, most originate from along the boundary between the monitored and unmonitored portions of the Sandhills population. We

**TABLE 1.** Models describing measures of performance for Red-cockaded Woodpeckers on private lands between 1980 and 2014, ranked by Akaike's information criterion corrected for small sample size ( $AIC_c$ ). SH = a categorical variable indicating whether Red-cockaded Woodpeckers bred on a property enrolled in the Safe Harbor program (vs. on a control property), Time = a continuous variable representing the number of years since enrollment in the Safe Harbor program, Group size = the number of adults plus helpers in a breeding group, Year = a categorical fixed effect representing the year of study, Laying date = square root transformed to meet normality assumptions and where day 1 is April 2, F-age = female age, M-age = male age, and %SH = the percentage of a breeding group's territory that was within a Safe Harbor property.  $K$  is the number of parameters,  $-2\text{Log}L$  is the maximized log-likelihood,  $\Delta AIC_c$  is the difference in  $AIC_c$  score relative to the top-ranked model, and  $w_i$  is the model weight. For brevity, only null models and alternative models with  $\Delta AIC_c \leq 2$  are shown.

Performance measure	Model	$K$	$-2\text{Log}L$	$\Delta AIC_c$	$w_i$
Cluster abandonment	SH + Time + SH*Time	4	969.33	0.00 <sup>a</sup>	0.54
	SH + Time + SH*Time + %SH + %SH*Time	6	972.02	0.34	0.46
	Null	1	1,004.27	24.90	0.00
Laying date	SH + Time + SH*Time + Group size + Year + F-Age + M-Age	8	2,761.53	0.00 <sup>b</sup>	0.83
	Null	1	3,171.74	326.39	0.00
Clutch size	SH + Time + SH*Time + Laying date + M-Age + F-Age	7	2,926.33	0.00 <sup>c</sup>	0.53
	SH + Time + SH*Time + Group size + Laying date + M-Age + F-Age	8	2,925.60	1.31	0.28
	Null	1	3,191.76	253.31	0.00
Breeding failure	SH + Time + SH*Time + Group size + Laying date + M-Age + F-Age	8	1,082.19	0.00 <sup>d</sup>	0.68
	SH + Time + SH*Time + %SH + %SH*Time + Group size + Laying date + M-Age + F-Age	10	1,079.70	1.59	0.31
	Null	1	1,261.25	164.90	0.00
Brood reduction	SH + Time + SH*Time + Group size + Laying date + M-Age + F-Age	8	1,778.57	0.00 <sup>e</sup>	0.75
	Null	1	1,975.03	181.87	0.00
Productivity	SH + Time + SH*Time + Group size + Laying date + M-Age + F-Age + Clutch size	9	3,011.35	0.00 <sup>f</sup>	0.64
	SH + Time + SH*Time + %SH + %SH*Time + Group size + Laying date + M-Age + F-Age + Clutch size	11	3,008.69	1.44	0.31
	Null	1	3,423.81	396.26	0.00

<sup>a</sup>  $AIC_c$  of the top-ranked model = 979.37.  
<sup>b</sup>  $AIC_c$  of the top-ranked model = 2,851.38.  
<sup>c</sup>  $AIC_c$  of the top-ranked model = 2,940.50.  
<sup>d</sup>  $AIC_c$  of the top-ranked model = 1,100.37.  
<sup>e</sup>  $AIC_c$  of the top-ranked model = 1,794.75.  
<sup>f</sup>  $AIC_c$  of the top-ranked model = 3,031.56.

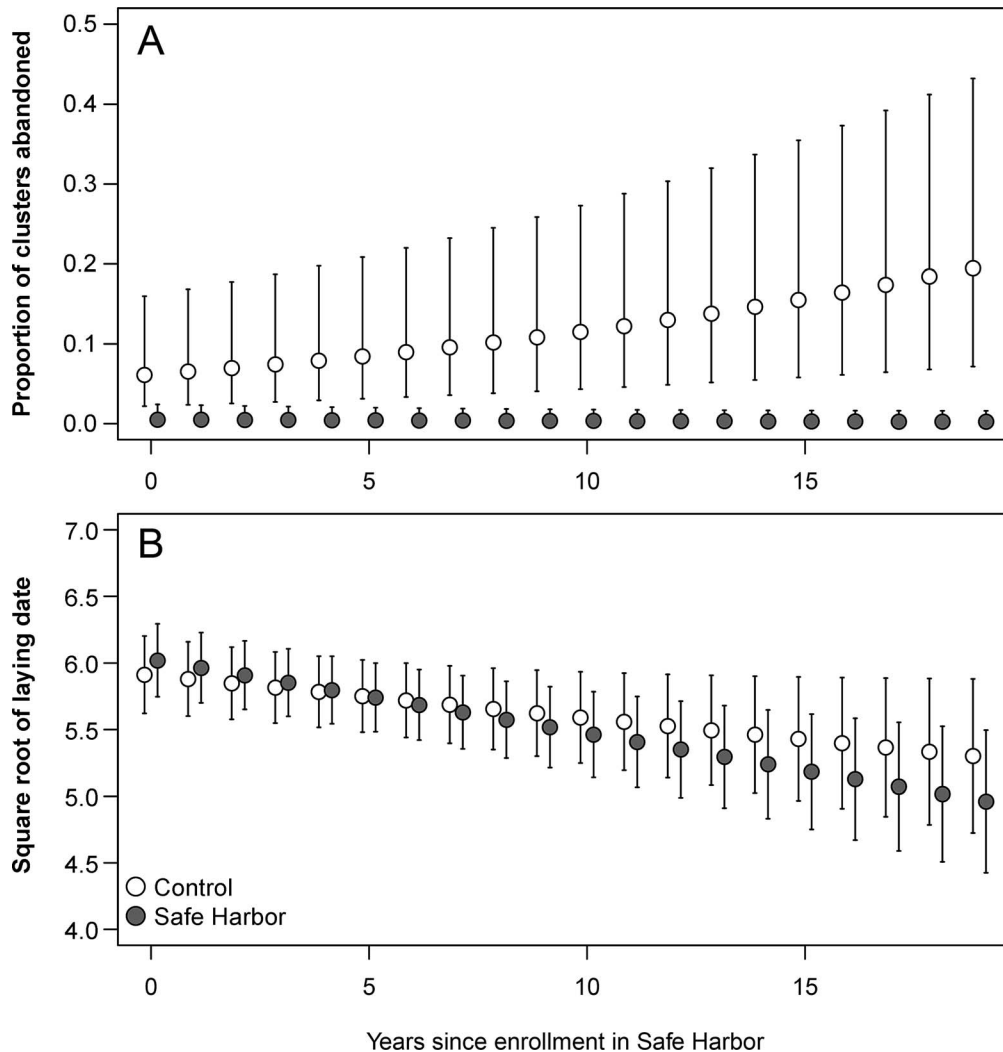
were confident that any effects of dispersal out of the study area would be minimal because the study area was located at the farthest distance from this boundary within the monitored portion of the population. When a chi-square statistic was significant ( $P < 0.05$ ), we calculated standardized residuals to determine whether either survival or emigration occurred significantly more or less than expected. Standardized residuals  $\geq 1.96$  were considered significant at  $P = 0.05$  (Sheskin 2003).

## RESULTS

We monitored 55 RCW clusters from 1980 to 2014 (30 Safe Harbor and 25 control). We collected between 2 and 24 yr of pre-enrollment data (mean = 18.2 yr) and between 11 and 19 yr of post-enrollment data (mean = 15.6 yr) for each cluster. Variation among clusters in the amount of

data collected pre- and post-enrollment was due to variation in enrollment dates of properties into Safe Harbor.

For most of the measures of breeding performance considered in our study, the model including year received less support from the data than the null model ( $\Delta AIC_c > 2$ ; Table 1). Thus, we pooled data across years for subsequent analysis. The one exception was laying date; the model in which laying date varied as a function of year alone received more support from the data than the null model ( $\Delta AIC_c = 67.10$ ), and thus year was included in all subsequent analysis of this variable. Many of the top-ranked models in our candidate sets were uninformative because they contained an uninformative parameter (Arnold 2010; Table 1). For brevity, unless stated otherwise, we report only informative models.



**FIGURE 2.** (A) Probability of cluster occupancy (mean  $\pm$  95% CI) by Red-cockaded Woodpeckers, and (B) laying dates of Red-cockaded Woodpeckers (mean  $\pm$  95% CI) monitored on properties enrolled in the Safe Harbor program and on control properties in North Carolina, USA, relative to the number of years since the initiation of the Safe Harbor program in 1995 (time zero). Data were collected between 1980 and 2014 (data collected before program initiation were assigned a value of zero). Data points are predicted values derived from mixed models that accounted for random effects and site-specific covariates.

### Cluster Abandonment

Model estimates from the top-ranked model (Table 1) indicated that cluster abandonment on control properties increased by  $\sim 14\%$  over the 19-yr period to 2014 following initiation of Safe Harbor in 1995 (pre-initiation:  $\beta = 0.06$ , 95% CI = 0.02–0.16; 19 yr post-initiation:  $\beta = 0.20$ , 95% CI = 0.07–0.43; Figure 2A). In contrast, cluster abandonment remained constant over time and at  $\sim 0$  on Safe Harbor properties (pre-initiation:  $\beta = 0.01$ , 95% CI = 0.00–0.02; 19 yr post-initiation:  $\beta = 0.00$ , 95% CI = 0.00–0.02). Model estimates indicated that temporal changes in abandonment between Safe Harbor and control properties were significantly different ( $\beta_{\text{control}} = 0.11$ , 95% CI = 0.03–0.17).

### Laying Date

Model estimates from the top-ranked model (Table 1) indicated that birds initiated clutches earlier in the season as group size increased ( $\beta = -0.13$ , 95% CI =  $-0.22$  to  $-0.04$ ), as female breeder age increased ( $\beta = -0.10$ , 95% CI =  $-0.13$  to  $-0.07$ ), and as male breeder age increased ( $\beta = -0.03$ , 95% CI =  $-0.06$  to  $-0.01$ ). Model estimates also indicated that, following the initiation of Safe Harbor in 1995, the laying date on Safe Harbor properties advanced significantly, by 16.1 days over the 19-yr period to 2014 (pre-initiation:  $\beta = 37.36$ , 95% CI = 34.03–40.85; 19 yr post-initiation:  $\beta = 21.24$ , 95% CI = 16.19–26.97; Figure 2B). In comparison, laying date advanced by 11.6 days on control properties (pre-initiation:  $\beta = 36.49$ , 95% CI =



32.94–40.22; 19 yr post-initiation:  $\beta = 24.85$ , 95% CI = 19.54–30.80). However, the 95% CI of the model estimate of the difference in temporal change in laying date between Safe Harbor and control properties slightly overlapped zero ( $\beta_{\text{control}} = 0.02$ , 95% CI = –0.00 to 0.05).

### Clutch Size

Model estimates from the top-ranked model (Table 1) suggested that clutch size decreased seasonally ( $\beta = -0.01$ , 95% CI = –0.01 to –0.00). Both female and male breeder age had a weak positive effect on clutch size (female:  $\beta = 0.01$ , 95% CI = –0.01 to 0.02; male:  $\beta = 0.01$ , 95% CI = –0.01 to 0.02). Clutch size did not change significantly over the 19-yr period following the initiation of Safe Harbor for birds breeding on either Safe Harbor (pre-initiation:  $\beta = 3.54$ , 95% CI = 3.03–4.12; 19 yr post-initiation:  $\beta = 3.44$ , 95% CI = 2.78–4.24) or control properties (pre-initiation:  $\beta = 3.46$ , 95% CI = 2.95–4.06; 19 yr post-initiation:  $\beta = 3.48$ , 95% CI = 2.74–4.42).

### Breeding Failure

Model estimates from the top-ranked model (Table 1) suggested that breeding failure increased seasonally (laying date:  $\beta = 0.03$ , 95% CI = 0.01–0.04), declined with group size ( $\beta = -0.40$ , 95% CI = –0.64 to –0.15), and increased with male breeder age ( $\beta = 0.08$ , 95% CI = 0.02–0.15). Female breeder age had a weak effect on breeding failure ( $\beta = -0.03$ , 95% CI = –0.11 to 0.04). The probability of breeding failure did not change significantly over the 19-yr period to 2014 following the initiation of Safe Harbor in 1995 for birds breeding on either Safe Harbor (pre-initiation:  $\beta = 0.25$ , 95% CI = 0.13–0.44; 19 yr post-initiation:  $\beta = 0.26$ , 95% CI = 0.11–0.50) or control properties (pre-initiation:  $\beta = 0.16$ , 95% CI = 0.07–0.32; 19 yr post-initiation:  $\beta = 0.28$ , 95% CI = 0.11–0.54).

### Brood Reduction

Model estimates from the top-ranked model (Table 1) suggested that brood reduction increased as group size decreased ( $\beta = -0.40$ , 95% CI = –0.53 to –0.27). There was also weak evidence for an effect of laying date and male and female breeder age on brood reduction (laying date:  $\beta = -0.00$ , 95% CI = –0.01 to 0.01; male age:  $\beta = -0.00$ , 95% CI = –0.04 to 0.03; female age:  $\beta = 0.01$ , 95% CI = –0.03 to 0.05). Model estimates indicated that brood reduction increased nonsignificantly over the 19-yr period following the initiation of Safe Harbor for birds breeding on both Safe Harbor (pre-initiation:  $\beta = 0.53$ , 95% CI = 0.42–0.64; 19 yr post-initiation:  $\beta = 0.67$ , 95% CI = 0.54–0.77) and control properties (pre-initiation:  $\beta = 0.53$ , 95% CI = 0.42–0.65; 19 yr post-initiation:  $\beta = 0.67$ , 95% CI = 0.53–0.80). These trends were equivalent between Safe Harbor and control properties ( $\beta_{\text{control}} = -0.01$ , 95% CI = –0.04 to 0.02).

### Productivity

Model estimates from the top-ranked model (Table 1) suggested that productivity increased as group size and clutch size increased (group size:  $\beta = 0.18$ , 95% CI = 0.12–0.25; clutch size:  $\beta = 0.07$ , 95% CI = 0.03–0.11) and decreased seasonally (laying date:  $\beta = -0.01$ , 95% CI = –0.01 to –0.00). Productivity increased nonsignificantly with female age ( $\beta = 0.01$ , 95% CI = –0.02 to 0.03) and decreased nonsignificantly with male age ( $\beta = -0.01$ , 95% CI = –0.03 to 0.01). Model estimates indicated that productivity decreased nonsignificantly over the 19-yr period following the initiation of Safe Harbor for birds breeding on both Safe Harbor (pre-initiation:  $\beta = 1.04$ , 95% CI = 0.78–1.37; 19 yr post-initiation:  $\beta = 0.76$ , 95% CI = 0.49–1.18) and control properties (pre-initiation:  $\beta = 1.14$ , 95% CI = 0.86–1.51; 19 yr post-initiation:  $\beta = 0.84$ , 95% CI = 0.56–1.26). These trends were equivalent between Safe Harbor and control properties ( $\beta_{\text{control}} = -0.00$ , 95% CI = –0.02 to 0.02).

### Survival and Emigration

Annual survival rates (survival events / mortality events + survival events) on Safe Harbor properties were 77% pre-initiation ( $n = 573$ ) and 79% post-initiation ( $n = 502$ ). On control properties, annual survival rates were 77% pre-initiation ( $n = 395$ ) and 75% post-initiation ( $n = 321$ ). Thus, survival was not significantly associated with treatment ( $\chi^2 = 2.43$ ,  $P > 0.05$ ). The annual proportion of females emigrating (emigration events / emigration events + retention events) from Safe Harbor properties was 24% pre-initiation ( $n = 305$ ) and 17% post-initiation ( $n = 272$ ). The annual rate of female emigration from control properties was 18% pre-initiation ( $n = 219$ ) and 21% post-initiation ( $n = 143$ ). Thus, emigration was also not significantly associated with treatment ( $\chi^2 = 4.48$ ,  $P > 0.05$ ).

## DISCUSSION

This study is the first comprehensive assessment of the efficacy of the Safe Harbor program toward improving the breeding success and persistence of an endangered species. By focusing on the earliest-established Safe Harbor program, our study offers the longest period of implementation across which to evaluate effects of the program on an imperiled species. Contrary to our predictions, we found no effect of enrollment in the program on clutch size, breeding failure, brood reduction, fledging success, or productivity of RCWs. However, temporal patterns in cluster abandonment following the initiation of Safe Harbor were significantly different between control and Safe Harbor properties; following initiation, the probability of cluster abandonment increased by ~14% over a 19-yr period on control properties, whereas it remained constant

and negligible on Safe Harbor properties over the same period. In addition, model estimates suggested that laying date advanced further on Safe Harbor properties than on control properties over the 19-yr period to 2014 following the initiation of Safe Harbor in 1995 (16.1 days vs. 11.6 days, respectively).

Prior to the initiation of Safe Harbor, the probability of cluster abandonment was ~6% higher on control properties compared with Safe Harbor properties, suggesting that the presence of RCWs influenced the likelihood that a landowner would enroll in Safe Harbor. Similarly, Zhang and Mehmood (2002) showed that Safe Harbor participants were more aware of whether or not RCWs were present and more likely to have active clusters on their properties compared with their control counterparts. Given that landowners face regulatory uncertainty when active RCW clusters occur on their property, we suggest that the higher likelihood of enrolling in Safe Harbor in the presence of occupied clusters reflects risk-averse behavior of landowners (Mehmood and Zhang 2005).

Enrollment in Safe Harbor reduced cluster abandonment compared with that observed on control properties, and thus reduced the loss of baseline groups. Following cavity tree loss to lightning strikes, disease, and windstorms, and cavity loss to enlargement by other cavity-excavating species (Conner et al. 2001, Harding and Walters 2002), the pool of old-growth pine trees suitable for new cavity excavation is often small and replacement trees are thus scarce. Furthermore, cavities typically require many years to excavate (Harding and Walters 2002). Under this scenario, cavity loss often results in cluster abandonment (Loeb et al. 1992). Thus, we suggest that the observed trends in cluster abandonment following the initiation of Safe Harbor were due to greater provisioning of artificial cavities that promoted continued occupancy on Safe Harbor properties (Copeyon et al. 1991); 87% of territories on Safe Harbor properties were provisioned with artificial cavities, compared with 68% of territories on control properties.

Overall, the laying date of RCWs advanced over the study period, supporting previous results from our study population (Schiegg et al. 2002, Garcia 2014). The RCW is one of many species in which an advanced laying date in response to increasing temperatures has been documented (e.g., Crick and Sparks 1999, Dunn and Winkler 1999, Both et al. 2004). The advancement in laying date was greater for birds on Safe Harbor properties compared with those on control properties. Previous research on this population has indicated that young females, inexperienced females, and experienced females breeding with a new mate advance their laying dates less than other birds in response to climate change (Schiegg et al. 2002). Thus, higher turnover of female breeders on control properties is a potential mechanism that could have produced the

difference that we observed. However, we found no association between enrollment in Safe Harbor and adult female emigration or survival, 2 mechanisms responsible for turnover rates. We found no evidence that this difference in the advancement of laying date resulted in any difference in reproductive performance, as might occur if changes in laying date disrupt temporal relationships between breeding and resource availability (Sanz et al. 2003, Dunn 2004, Visser et al. 2004). Similarly, Schiegg et al. (2002) and Garcia (2014) found that changes in laying date associated with climate change did not result in reduced breeding success in this population.

RCWs that bred on private lands in our study area experienced lower breeding productivity compared with those that bred on adjacent public lands (e.g., clutch size: private = 3.26, public = 3.37; average number of fledglings: private = 1.63, public = 1.82; J. Smith personal observation), where RCW habitat quality was higher (K. Brust personal observation). This suggests that foraging habitat quality was relatively poor on private lands, as productivity is correlated with foraging habitat quality both within the Sandhills (Walters et al. 2002) and range-wide (Davenport et al. 2000, McKellar et al. 2014). Thus, given that we found no effect of Safe Harbor on most measures of breeding performance, our results suggest that enrollment in Safe Harbor did not consistently result in the maintenance of higher-quality foraging habitat. Even if habitat quality had varied widely among sites, our BACI design should have detected a treatment effect if enrollment in Safe Harbor resulted in improved foraging habitat quality. One possible explanation for the lack of a Safe Harbor effect is that the habitat management standards used on Safe Harbor properties may not be effective for promoting productivity. The habitat targets employed in the private land standards differ from those for public lands, and, unlike the latter, are not correlated with RCW breeding performance (Walters et al. 2002, USFWS 2003).

That the program permits habitat management to vary substantially across properties may have contributed to the absence of an overall Safe Harbor effect. Lack of funding for habitat management may also have been a factor. Some funding for management activities, such as prescribed burning and hardwood midstory removal that improve foraging habitat quality, has been provided through various federal and state programs, including the Wildlife Habitat Incentive Program, Landowner Incentive Program, and Private Stewardship Grant Program. However, funding has been inconsistent and limited to a few large properties. Improving the productivity of RCWs on Safe Harbor properties through management of foraging habitat likely will require replacing the current habitat management guidelines with guidelines more similar to those applied to public lands and providing incentives to landowners to

apply them. This may not be a realistic goal, given the constraints on management of private lands. For example, prescribed burning, which is essential to maintaining high-quality foraging habitat (James et al. 1997), is not feasible on Safe Harbor properties in residential areas. The need to elevate outreach and education to private landowners with working forests, many of whom are enrolled in Safe Harbor, has been acknowledged by the North Carolina Sandhills Conservation Partnership. One outcome has been the Sandhills Prescribed Burn Association (PBA), which was created to provide technical assistance and leverage resources available to private landowners for prescribed burning. The PBA will undoubtedly encourage the reintroduction of prescribed fire to Safe Harbor properties located outside municipalities.

Given the funding and logistical obstacles associated with foraging habitat enhancement, artificial cavity provisioning has been the sole management effort pursued for many RCW clusters on private lands. The U.S. Fish and Wildlife Service, Federal Emergency Management Agency, and Natural Resource Conservation Service provided funding for cavity construction beginning in 1996 in response to loss of cavities to Hurricane Fran, but these monies were spent by the mid-2000s. Provisioning and maintenance of suitable artificial cavities within these same clusters on private lands, while facilitated by enrollment in the Safe Harbor program, has been funded largely by a nongovernmental organization over the last decade. Limited funding for cavity work has come from mitigation for property development.

## Conclusions

The initial Safe Harbor program in the North Carolina Sandhills clearly accomplished its immediate objective of alleviating conflict over RCW conservation. Widespread cutting of potential habitat that occurred prior to Safe Harbor ceased (Lueck and Michael 2003), many landowners enrolled in the program, and attitudes toward conservation changed quickly and have remained much more positive. The primary management activity conducted on Safe Harbor properties, provisioning of artificial cavities, has been effective in promoting cluster occupancy and retention of individual birds in territories. Thus, one can argue that the Safe Harbor program has played an important role in the retention of RCWs on private land since its inception 20 yr ago.

Importantly, this study highlights challenges to conservation-based objectives that may be common across Safe Harbor programs and other incentive programs focused on private lands. The efficacy of Safe Harbor, at least for RCWs, appears to be dependent on adequate funding and the implementation of appropriate habitat management techniques. Additional evaluation of Safe Harbor programs for a wide range of species in different geographic

locations will reveal the generality of these potential limitations. The challenge will be to adjust programs appropriately to increase engagement between private landowners, agencies, and biologists to meet conservation objectives.

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## LITERATURE CITED

- Arnold, T. W. (2010). Uninformative parameters and model selection using Akaike's Information Criterion. *The Journal of Wildlife Management* 74:1175–1178.
- Bolker, B. M., M. E. Brooks, C. J. Clark, S. W. Geange, J. R. Poulsen, M. H. H. Stevens, and J.-S. S. White (2009). Generalized linear mixed models: A practical guide for ecology and evolution. *Trends in Ecology & Evolution* 24:127–135.
- Bonnie, R. (1997). Safe harbor for the Red-cockaded Woodpecker. *Journal of Forestry* 95:17–22.
- Both, C., A. V. Artemyev, B. Blaauw, R. J. Cowie, A. J. Dekhuijzen, T. Eeva, A. Enemar, L. Gustafsson, E. V. Ivankina, A. Järvinen, N. B. Metcalfe, et al. (2004). Large-scale geographical variation confirms that climate change causes birds to lay earlier. *Proceedings of the Royal Society of London, Series B* 271: 1657–1662.
- Burnham, K. P., and D. R. Anderson (2002). *Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach*, second edition. Springer, New York, NY, USA.
- Carter, J. H., III, J. R. Walters, S. H. Everhart, and P. D. Doerr (1989). Restrictors for Red-cockaded Woodpecker cavities. *Wildlife Society Bulletin* 17:68–72.
- Conner, R. N., D. C. Rudolph, and J. R. Walters (2001). *The Red-cockaded Woodpecker: Surviving in a Fire-Maintained Ecosystem*. University of Texas Press, Austin, TX, USA.



- Convery, K. M., and J. R. Walters (2004). Red-cockaded Woodpecker home range and foraging partitions. In *Red-cockaded Woodpecker: Road to Recovery* (R. Costa and S. J. Daniels, Editors). Hancock House, Blaine, WA, USA. pp. 526–535.
- Copeyon, C. K., J. R. Walters, and J. H. Carter, III (1991). Induction of Red-cockaded Woodpecker group formation by artificial cavity construction. *The Journal of Wildlife Management* 55: 549–556.
- Crick, H. Q. P., and T. H. Sparks (1999). Climate change related to egg-laying trends. *Nature* 399:423.
- Davenport, D. E., R. A. Lancia, J. R. Walters, and P. D. Doerr (2000). Red-cockaded Woodpeckers: A relationship between reproductive fitness and habitat in the North Carolina Sandhills. *Wildlife Society Bulletin* 28:426–434.
- Dormann, C. F., J. Elith, S. Bacher, C. Buchmann, G. Carl, G. Carré, J. R. García Marquéz, B. Gruber, B. Lafourcade, P. J. Leitão, T. Münkemüller, et al. (2013). Collinearity: A review of methods to deal with it and a simulation study evaluating their performance. *Ecography* 36:27–46.
- Dunn, P. (2004). Breeding dates and reproductive performance. *Advances in Ecological Research* 35:69–87.
- Dunn, P. O., and D. W. Winkler (1999). Climate change has affected the breeding date of Tree Swallows throughout North America. *Proceedings of the Royal Society of London, Series B* 266:2487–2490.
- Garabedian, J. E., C. E. Moorman, M. N. Peterson, and J. C. Kilgo (2017). Use of LiDAR to define habitat thresholds for forest bird conservation. *Forest Ecology and Management* 399:24–36.
- Garcia, V. D. (2014). Lifetime fitness and changing life history traits in Red-cockaded Woodpeckers. Ph.D. dissertation, Virginia Polytechnic Institute and State University, Blacksburg, VA, USA.
- Harding, S. R., and J. R. Walters (2002). Processes regulating the population dynamics of Red-cockaded Woodpecker cavities. *The Journal of Wildlife Management* 66:1083–1095.
- James, F. C., C. A. Hess, and D. Kufirin (1997). Species-centered environmental analysis: Indirect effects of fire history on Red-cockaded Woodpeckers. *Ecological Applications* 7:118–129.
- Johnson, M. D. (2007). Measuring habitat quality: A review. *The Condor* 109:489–504.
- LaBranche, M. S., and J. R. Walters (1994). Patterns of mortality in nests of Red-cockaded Woodpeckers in the Sandhills of southcentral North Carolina. *The Wilson Bulletin* 106:258–271.
- Loeb, S. C., W. D. Pepper, and A. T. Doyle (1992). Habitat characteristics of active and abandoned Red-cockaded Woodpecker colonies. *Southern Journal of Applied Forestry* 16:120–125.
- Lueck, D., and J. A. Michael (2003). Preemptive habitat destruction under the Endangered Species Act. *Journal of Law and Economics* 46:27–60.
- McKellar, A. E., D. C. Kesler, R. J. Mitchell, D. K. Delaney, and J. R. Walters (2014). Geographic variation in fitness and foraging habitat quality in an endangered bird. *Biological Conservation* 175:52–64.
- Mehmood, S. R., and D. Zhang (2005). Determinants of forest landowner participation in the Endangered Species Act Safe Harbor program. *Human Dimensions of Wildlife* 10:249–257.
- Perrins, C. M. (1970). The timing of birds' breeding seasons. *Ibis* 112:242–255.
- Sansom, A., J. W. Pearce-Higgins, and D. J. T. Douglas (2016). Negative impact of wind energy development on a breeding shorebird assessed with a BACI study design. *Ibis* 158:541–555.
- Sanz, J. J., J. Potti, J. Moreno, S. Merino, and O. Frías (2003). Climate change and fitness components of a migratory bird breeding in the Mediterranean region. *Global Change Biology* 9:461–472.
- SAS Institute (1990). *SAS-STAT User's Guide, Version 6*, fourth edition. SAS Institute, Cary, NC, USA.
- Schiegg, K., G. Pasinelli, J. R. Walters, and S. J. Daniels (2002). Inbreeding and experience affect response to climate change by endangered woodpeckers. *Proceedings of the Royal Society of London, Series B* 269:1153–1159.
- Sheskin, D. (2003). *Handbook of Parametric and Nonparametric Statistical Procedures*. Chapman and Hall/CRC, Boca Raton, FL, USA.
- Stephens, J. L., I. J. Ausprey, N. E. Seavy, and J. D. Alexander (2015). Fire severity affects mixed broadleaf-conifer forest bird communities: Results for 9 years following fire. *The Condor: Ornithological Applications* 117:430–446.
- Trainor, A. M., J. R. Walters, D. L. Urban, and A. Moody (2013). Evaluating the effectiveness of a Safe Harbor program for connecting wildlife populations. *Animal Conservation* 16: 610–620.
- USFWS (U.S. Fish and Wildlife Service) (2003). *Recovery Plan for the Red-Cockaded Woodpecker (*Picooides borealis*): Second Revision*. U.S. Fish and Wildlife Service, Atlanta, GA, USA.
- USGAO (U.S. General Accounting Office) (1994). *Endangered Species Act: Information on Species Protection on Nonfederal Lands*. GAO/RCED-95-16, GAO, Washington, DC, USA.
- Visser, M. E., C. Both, and M. M. Lambrechts (2004). Global climate change leads to mistimed avian reproduction. *Advances in Ecological Research* 35:89–110.
- Walters, J. R. (1991). Application of ecological principles to the management of endangered species: The case of the Red-cockaded Woodpecker. *Annual Review of Ecology and Systematics* 22:505–523.
- Walters, J. R., and V. Garcia (2016). Red-cockaded Woodpeckers: Alternative pathways to breeding success. In *Cooperative Breeding in Vertebrates: Studies of Ecology, Evolution, and Behavior* (W. D. Koenig and J. L. Dickinson, Editors). Cambridge University Press, Cambridge, UK. pp. 58–76.
- Walters, J. R., S. J. Daniels, J. H. Carter, III, and P. D. Doerr (2002). Defining quality of Red-cockaded Woodpecker foraging habitat based on habitat use and fitness. *The Journal of Wildlife Management* 66:1064–1082.
- Walters, J. R., P. D. Doerr, and J. H. Carter, III (1988). The cooperative breeding system of the Red-cockaded Woodpecker. *Ethology* 78:275–305.
- Wilcove, D. S., and J. Lee (2004). Using economic and regulatory incentives to restore endangered species: Lessons learned from three new programs. *Conservation Biology* 18:639–645.
- Winder, V. L., A. J. Gregory, L. B. McNew, and B. K. Sandercock (2015). Responses of male Greater Prairie-Chickens to wind energy development. *The Condor: Ornithological Applications* 117:284–296.
- Zhang, D., and S. R. Mehmood (2002). Safe harbor for the Red-cockaded Woodpecker: Private forest landowners share their views. *Journal of Forestry* 100:24–29.